

COMPARATIVE POLLEN MORPHOLOGY OF THE AMERICAN MYRISTICACEOUS GENERA *COMPSONEURA* AND *VIOLA*¹

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ABSTRACT

Pollen of the American myristicaceous genera *Compsonaura* and *Viola* was studied with light, scanning electron, and transmission electron microscopy. Formal generic pollen descriptions are provided for each of these genera. Study of the pollen of these two genera reveals that they possess a number of similar palynological features, including sulcate apertures, reticuloid to reticulate exine sculpturing that sometimes consists of banded or beaded muri, a columellate interstitium with columellae frequently hanging from the tectum or only weakly attached to the nexine, and tectate-perforate to semitectate pollen grains. Pollen of *Compsonaura*, however, can be distinguished from that of *Viola* by (1) its nexine which is generally twice as thick as that in *Viola*, (2) its consistently more or less solid, nonlamellate nexine, and (3) its consistently inconspicuous intra-exinous, sexinous cavities. Within *Compsonaura*, pollen of section *Coniostele* is decidedly more advanced than that of section *Compsonaura*. *Viola* exhibits a wide range of exine sculpturing patterns, allowing recognition of three basic pollen types. Species of Pollen Type I have basically tectate-perforate grains although sometimes their pollen may be more or less reticuloid, and the exine surface or muri are usually psilate. Pollen Type II is characterized by tectate-perforate to semitectate grains which have banded to beaded muri, while Type III pollen grains are semitectate-reticulate with psilate muri.

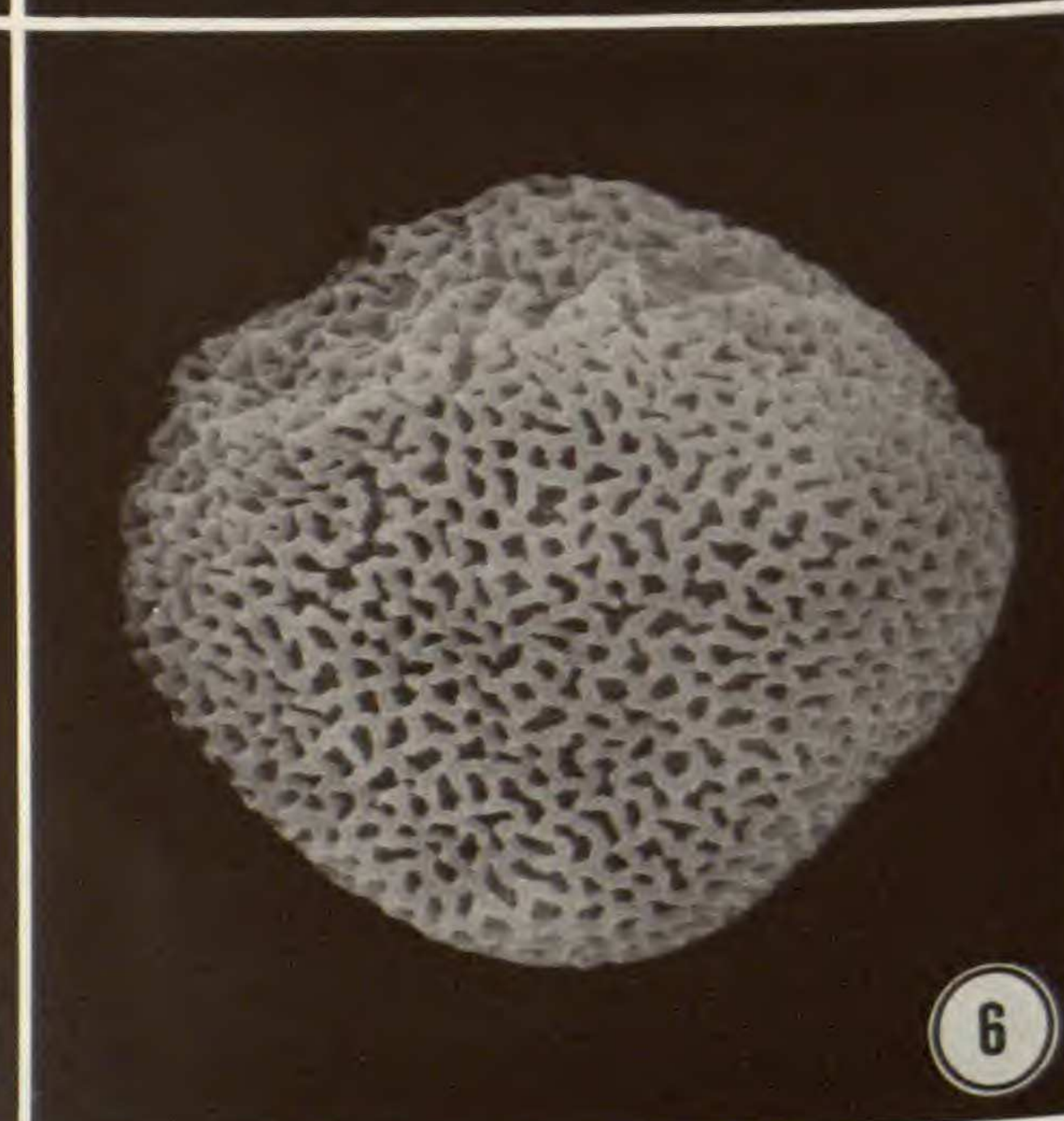
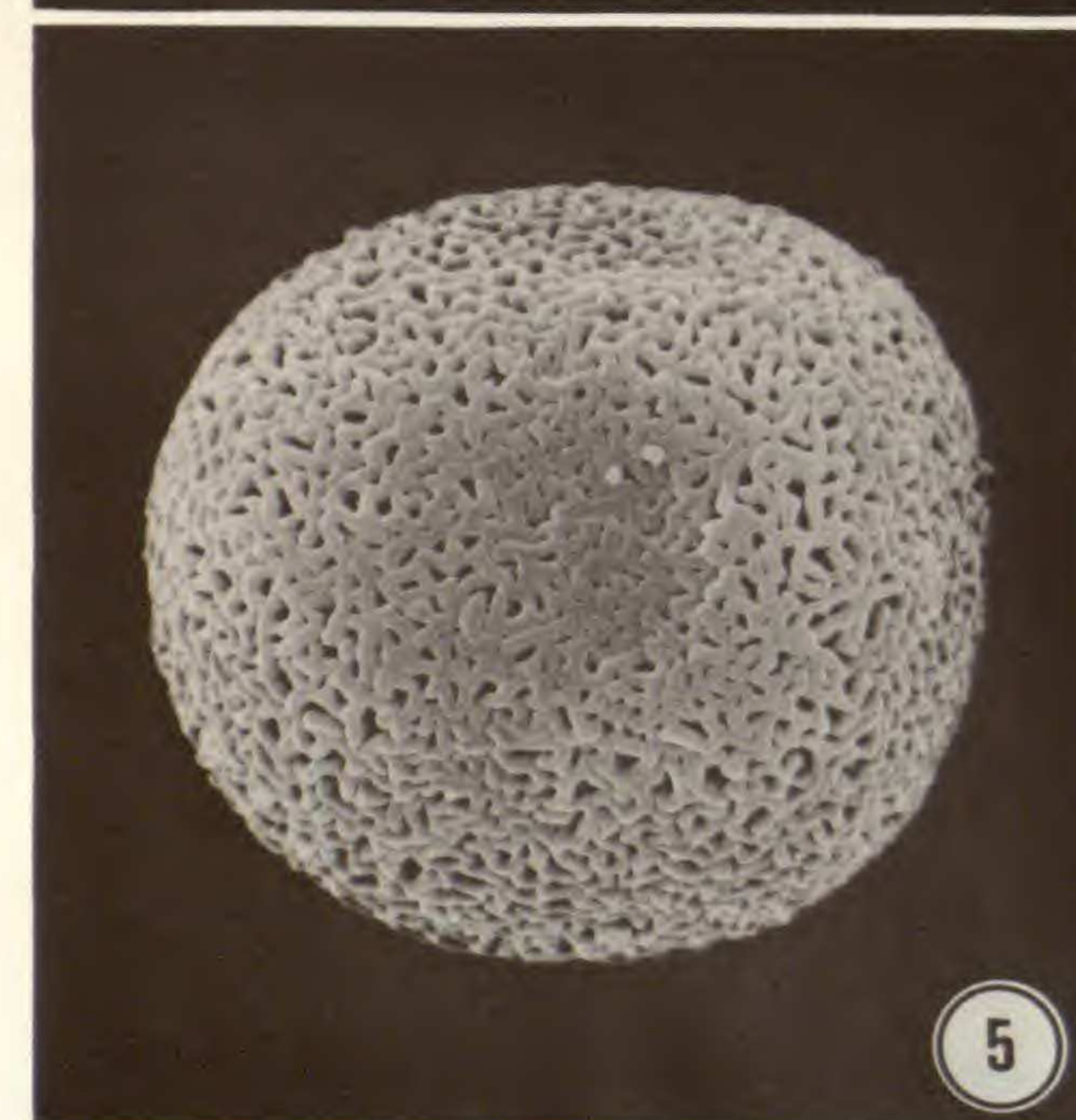
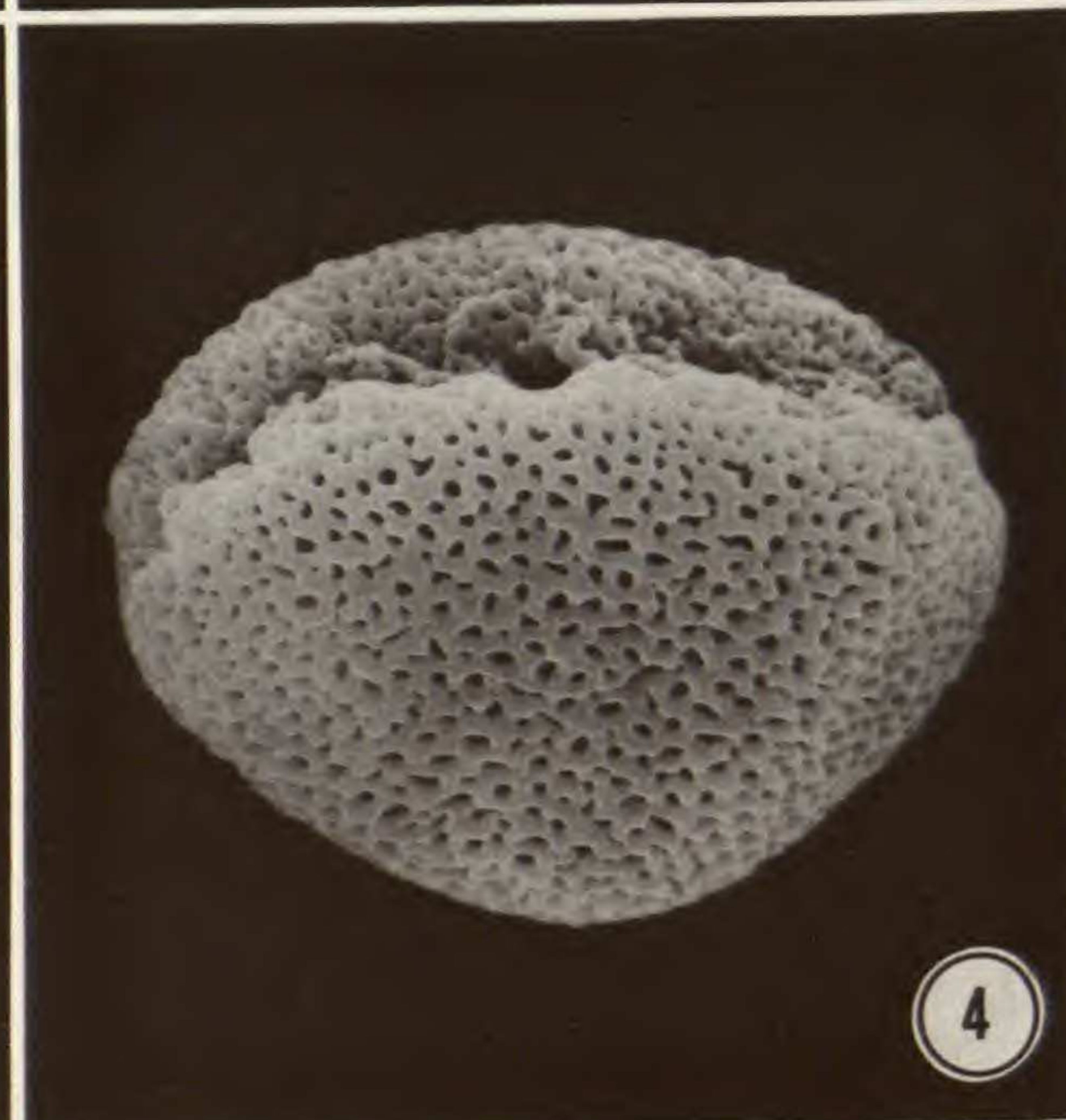
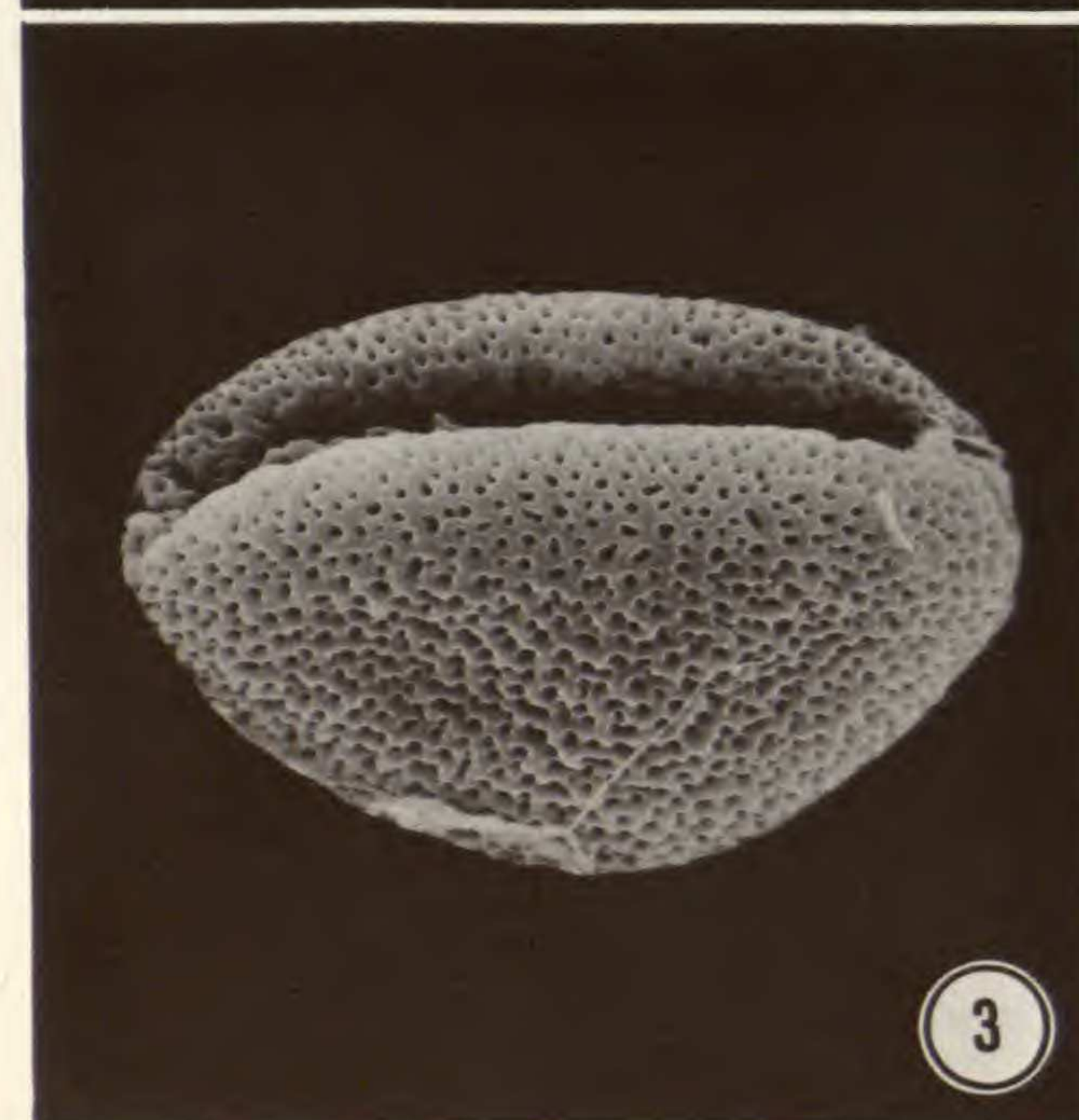
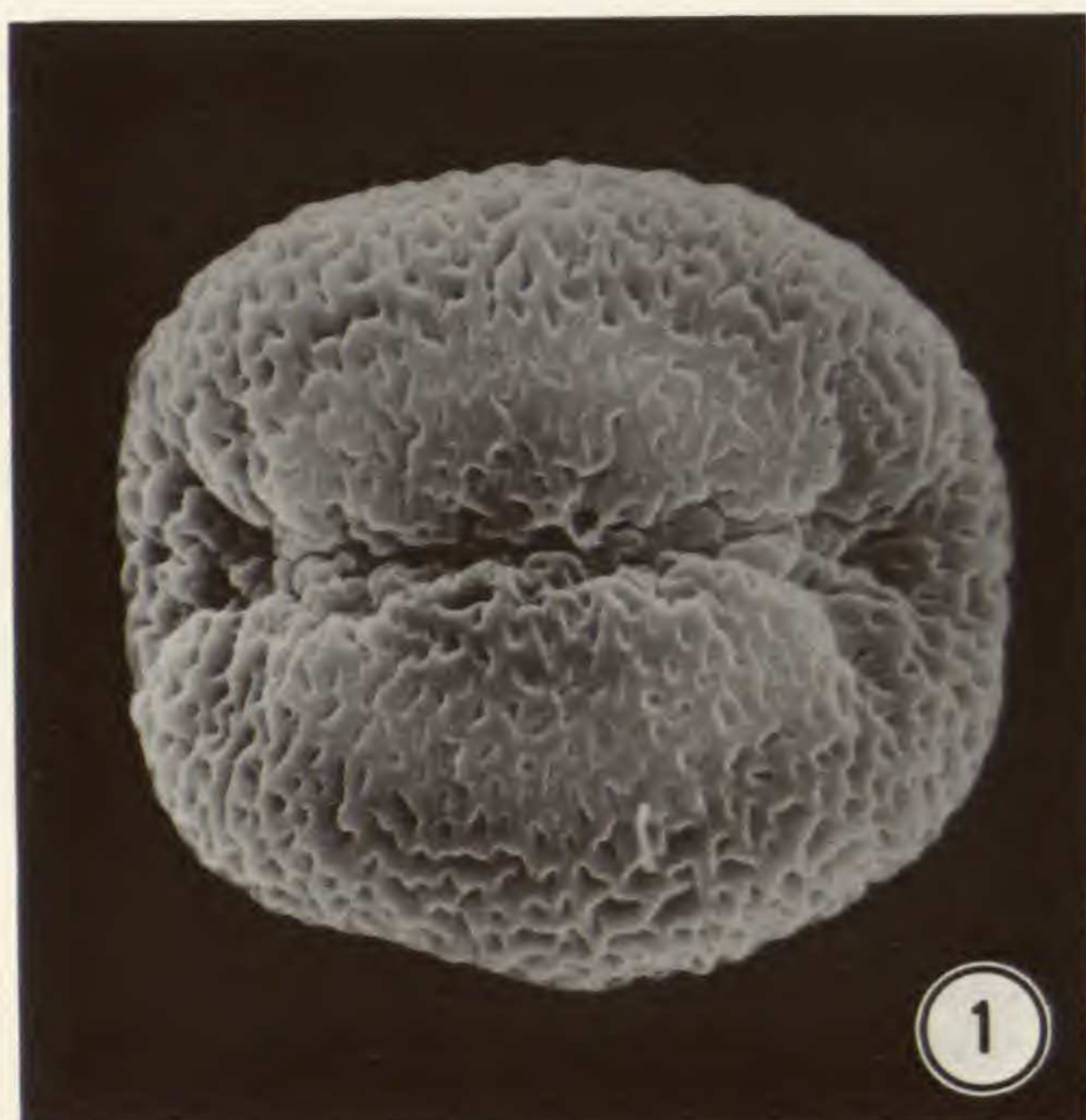
This is the fourth paper in a series dealing with the comparative pollen morphology of the family Myristicaceae. In previous papers we have already dealt with the pollen of the Madagascan (Walker & Walker, *Grana*, in press) and mainland African (Walker & Walker, *Amer. J. Bot.*, 1, in press) genera of Myristicaceae, and with the American myristicaceous genera *Dialyanthera*, *Iryanthera*, and *Osteophloeum* (Walker & Walker, *Amer. J. Bot.*, 2, in press). We are concerned in this paper with the pollen of the two remaining genera of American Myristicaceae—*Compsonaura* and *Viola*. We intend to examine the pollen of the Asian genera of Myristicaceae in subsequent papers.

In the most recent revision of the American Myristicaceae, Smith (1938) recognized 8 species of *Compsonaura* and 38 species of *Viola*. Since then 2 additional species of *Compsonaura* and 9 more of *Viola* have been described, so that at present there are 10 species of *Compsonaura* and approximately 50 species of *Viola*. *Compsonaura* and *Viola* range from southern Mexico to northern South America, where most of their species occur.

After the material and methods section, formal generic pollen descriptions are provided for both of the genera studied. This is followed by a discussion of the palynological features of these two genera, such as aperture type, exine sculptur-

¹ We thank the directors of the following herbaria for allowing us to collect palynological material from their collections: Arnold Arboretum, Harvard University; Gray Herbarium, Harvard University; Royal Botanic Gardens, Kew; Botaniska Institutionen, Naturhistoriska Riksmuseet, Stockholm; and Rijksherbarium, Leiden. We are especially grateful to Keith Ferguson (Kew), B. Sparre, S. Nilsson, and J. Pragłowski (Stockholm), and J. Muller (Leiden) for their help during our visits to their respective institutions. This work was supported by U.S. National Science Foundation grants GB-35475, BMS 75-10438 (subsequently DEB 75-10438), BMS 75-02883, and DEB 79-04213 to James W. Walker.

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ing, exine structure, and so forth. The pollen of *Compsonaura* is then compared as a whole with the pollen of *Virola* in the conclusions section of the paper.

MATERIAL AND METHODS

Pollen for study was taken from herbarium sheets at the Arnold Arboretum, Harvard University (A); the Gray Herbarium, Harvard University (GH); the Royal Botanic Gardens, Kew (K); the Botaniska Institutionen, Naturhistoriska Riksmuseet, Stockholm (S); and the Rijksherbarium, Leiden (L). Voucher specimens and the senior author's palynological accession number (preceded by a "p") are listed for each collection studied after the generic pollen descriptions, and indication is given if the pollen was studied by scanning electron microscopy of the surface (SEM) or of sectioned material (SEM-X) or by transmission electron microscopy (TEM). An attempt was made to study pollen from as many collections annotated by A. C. Smith or cited by him (Smith, 1938, 1950) as possible. In all we examined pollen of 7 of the 10 species of *Compsonaura* and 32 of the nearly 50 species of *Virola*. Terminology follows Walker & Doyle (1975), Walker (1974, 1976), and Walker & Walker (in press, 1, 2, 3).

Pollen was prepared for light microscopy, scanning electron microscopy, and transmission electron microscopy essentially by the same methods previously outlined (Walker & Walker, in press, 1, 2).

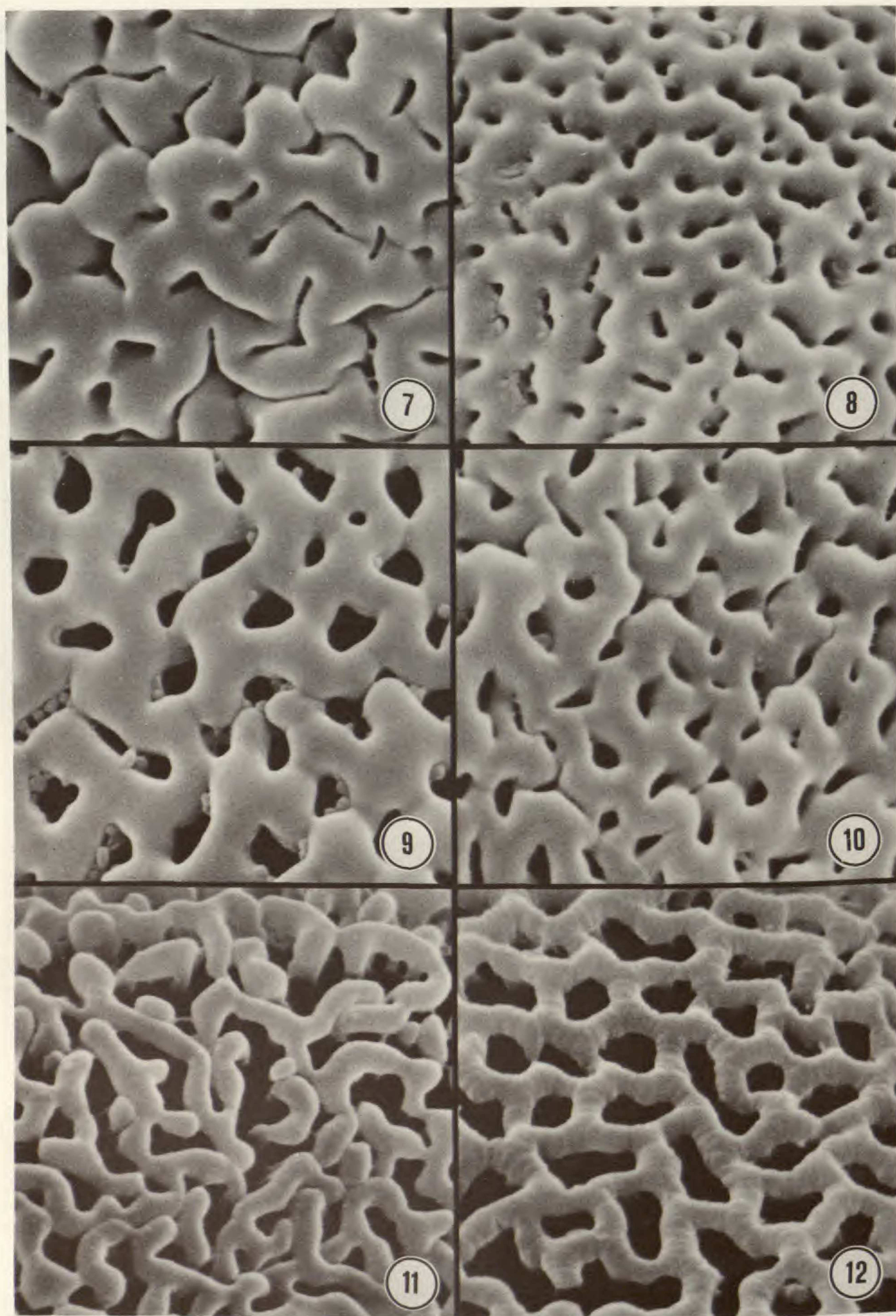
GENERIC POLLEN DESCRIPTIONS

Compsonaura Warburg (Figs. 1–24)

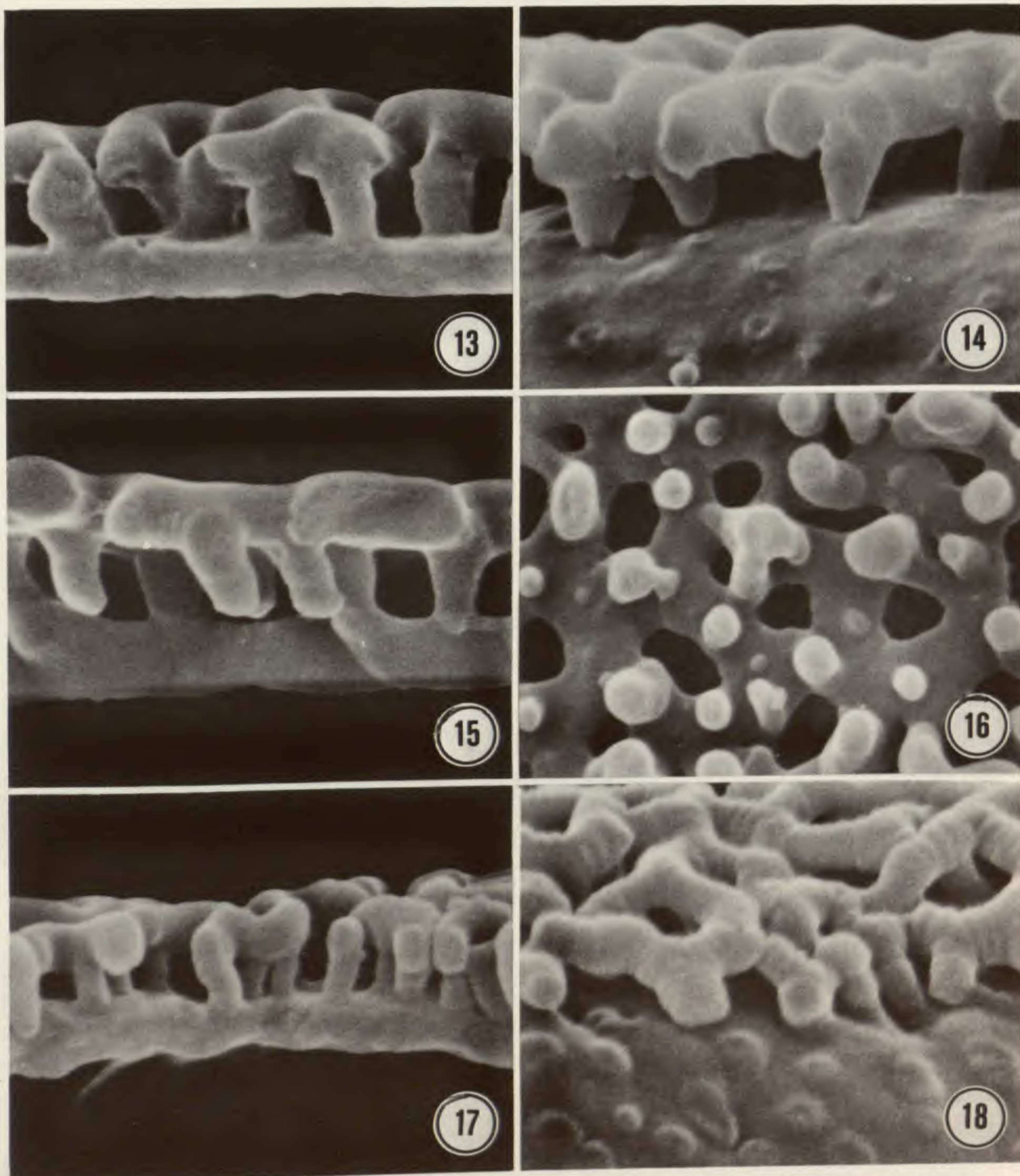
Pollen.—Apertures sulcate, sharply delimited externally. Shape usually boat-shaped, occasionally almost globose-spherical, frequently more or less triangular in outline and often more or less straight on the apertural face and markedly convex on the opposite face. Polarity heteropolar. Symmetry bilateral. Size medium-sized to small (mean 24 μm , range 21–27 μm). Pollen-Unit monads. Exine Sculpturing mostly reticuloid, less commonly definitely reticulate and then sometimes with finely banded muri. Exine Structure columellate (columellae weakly attached to the nexine), tectate-perforate or less commonly semitectate; non-apertural exine about 1.50 μm thick, with an average (about 32% of total exine thickness), essentially solid nexine, an average to moderately thick (about 39% of total exine thickness) interstitium, and an average (about 29% of total exine thickness) tectum, sexine infrequently with small, spherical, intra-exinous cavities; apertural exine with an extremely to very thin nexine and a greatly reduced and much disorganized sexine. Exine Stratification wholly ektexinous; endexine none.

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FIGURES 1–6. Whole pollen grains of *Compsonaura* Warburg (1–4, Section *Compsonaura*; 5–6, Section *Coniostele* Warburg).—1–2. *C. capitellata* (A. DC.) Warburg (*Klug* 2130, 1, P-1956; 2, P-895), 1, apertural side, 2, nonapertural side; both $\times 2,500$.—3. *C. debilis* (A. DC.) Warburg (*Ducke* 36, P-2707); $\times 2,500$.—4. *C. sprucei* (A. DC.) Warburg (*J. D. Smith* 5256, P-1948); $\times 2,100$.—5. *C. excelsa* A. C. Smith (*Skutch* 2791, P-1950); $\times 3,000$.—6. *C. ulei* Warburg (*Prance et al.* 8562, P-1954); $\times 2,200$.

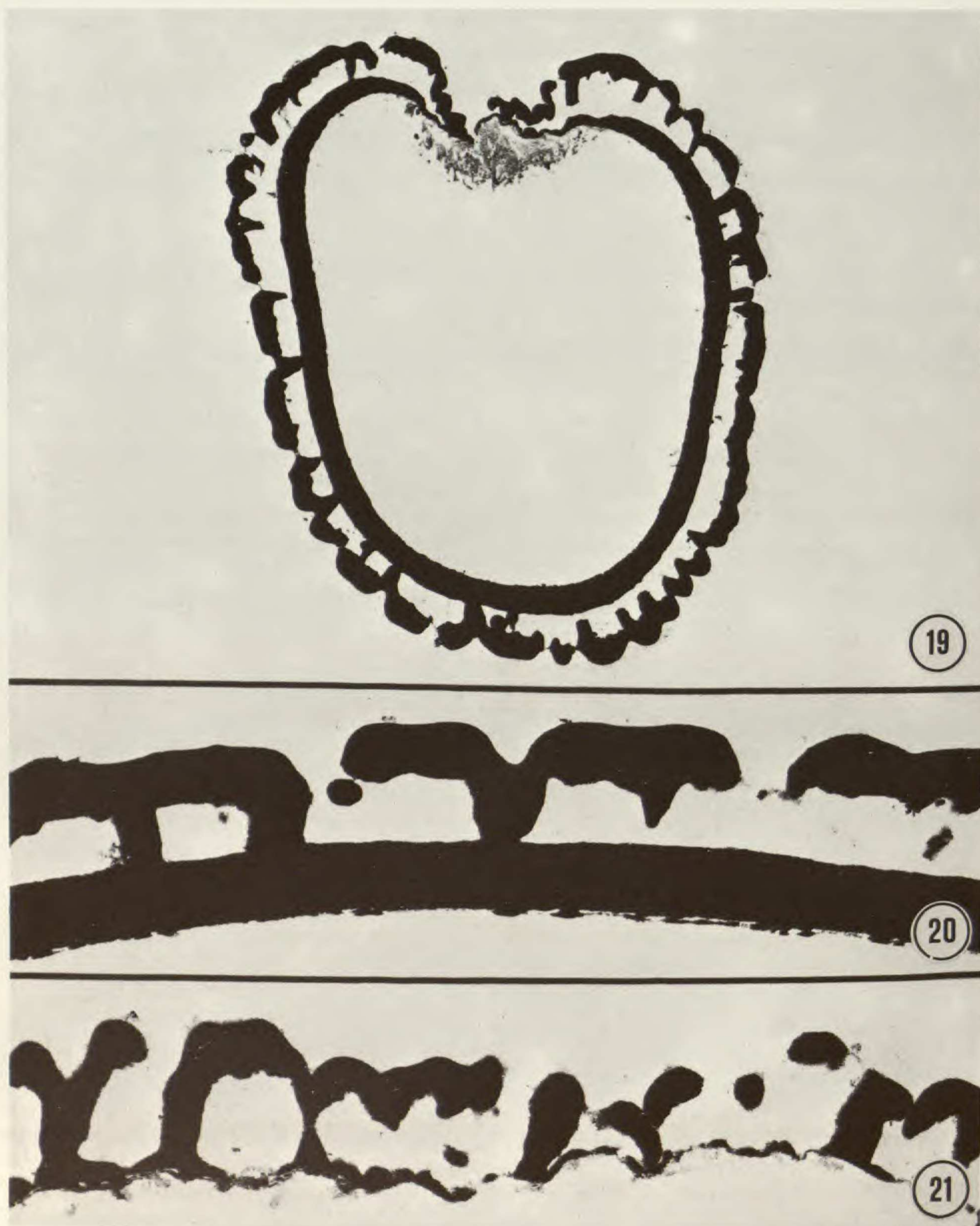


FIGURES 7-12. Exine surface of *Compsoeura* Warburg (7-10. Section *Compsoeura*; 11-12. Section *Coniosteale* Warburg).—7. *C. capitellata* (A. DC.) Warburg (*Klug* 2130, P-895).—8. *C. racemosa* Ducke (*Krukoff* 8754, P-2708).—9. *C. sprucei* (A. DC.) Warburg (*J. D. Smith* 5256, P. 1948).—10. *C. debilis* (A. DC.) Warburg (*Ducke* 36, P-2707).—11. *C. excelsa* A. C. Smith (*Skutch* 2791, P-1950).—12. *C. ulei* Warburg (*Prance et al.* 8562, P-1954). All $\times 12,000$.

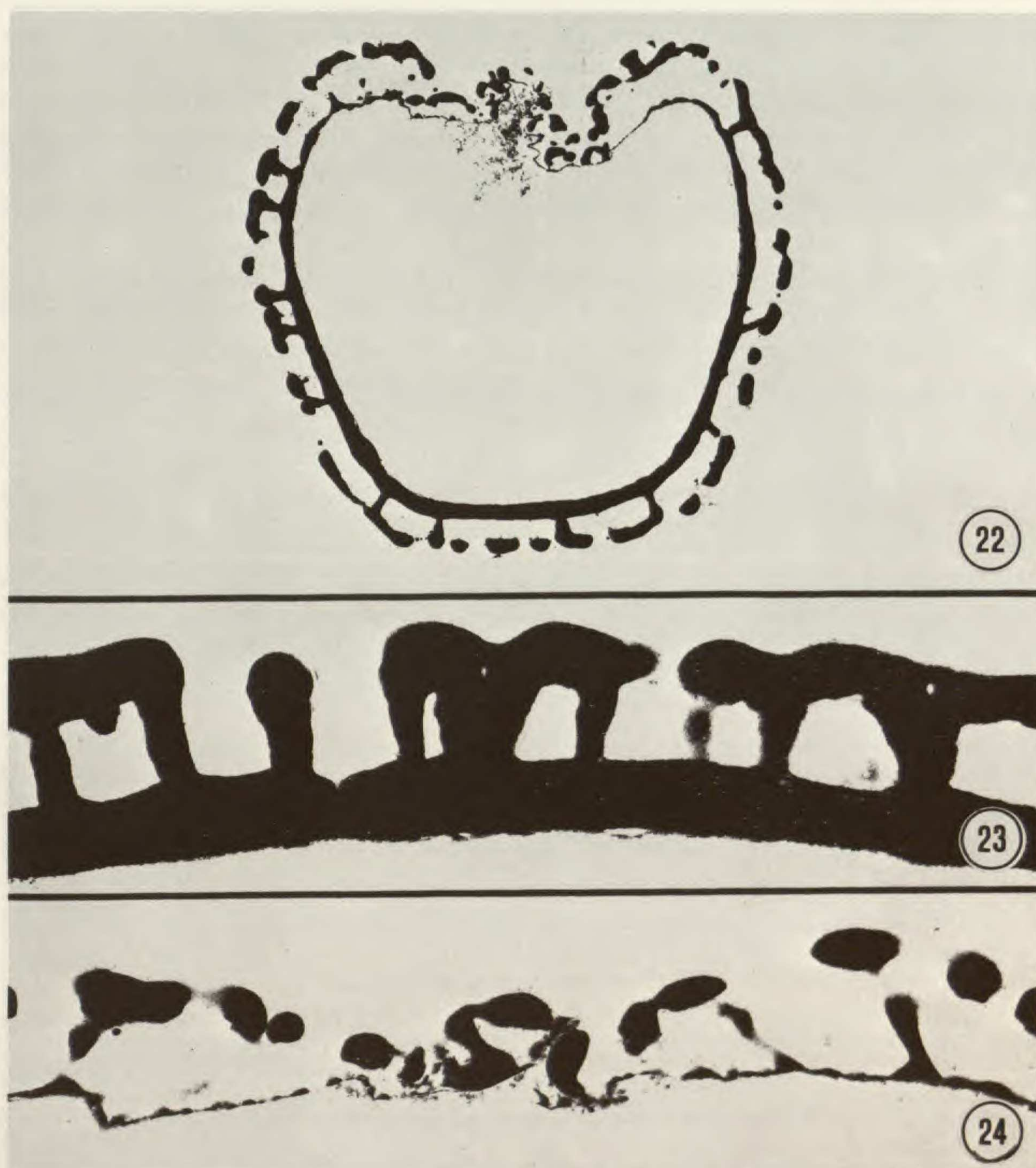


FIGURES 13–18. SEM nonapertural exine sections of *Compsonneura* Warburg (13–16, Section *Compsonneura*; 17–18, Section *Coniostele* Warburg).—13. *C. debilis* (A. DC.) Warburg (*Ducke* 36, *Compsonneura*; 17–18, Section *Coniostele* Warburg).—14. *C. capitellata* (A. DC.) Warburg (*Klug* 2130, P-895), note circular depressions left on surface of nexine by separation of weakly attached columellae.—15–16. *C. sprucei* (A. DC.) Warburg (*J. D. Smith* 5256, P-1948), 15, cross-section, note columellae pendulous from inner surface of tectum, 16, tangential section through interstitium looking at inner surface of tectum, note granules on inner surface of tectum mixed in with columellae.—17. *C. excelsa* A. C. Smith (*Skutch* 2791, P-1950).—18. *C. ulei* Warburg (*Prance et al.* 8562, P-1954), note circular depressions in surface of nexine where columellae were attached to nexine. All $\times 16,000$.

Specimens Examined.—*Compsonneura capitellata* (A. DC.) Warburg, *Klug* 2130 (GH), P-895 (SEM, SEM-X, TEM), (K), P-1956 (SEM); *Ducke* I.A.N. 143 (K), P-1953. *C. debilis* (A. DC.) Warburg, *Ducke* 36 (A), P-894, (K), P-1951 (SEM, TEM), (S), P-2707 (SEM, SEM-X). *C. excelsa* A. C. Smith, *Skutch* 2791 (GH), P-1133 (SEM), (K), P-1950 (SEM, SEM-X). *C. mutisii* A. C. Smith, *Haught Smith*, *Skutch* 2791 (GH), P-1133 (SEM), (K), P-1950 (SEM, SEM-X). *C. racemosa* *Ducke*, *Krukoff* 8754 (A), P-1135, (K), P-1952 (SEM), (S), P-1733 (A), P-1134 (SEM). *C. sprucei* (A. DC.) Warburg, *Bartlett* 11330 (A), P-892; *Bangham* 357 (A), P-893; *J.* 2708 (SEM).



FIGURES 19-21. TEM exine sections of *Compsonneura capitellata* (A. DC.) Warburg (Klug 2130, P-895).—19. Whole grain exine section, showing aperture at top and partly acetolysis-resistant intine beneath, $\times 4,600$.—20. Nonapertural exine section, showing average, essentially solid nexine, average to moderately thick columellate interstitium, and average tectum, $\times 15,000$.—21. Apertural exine section, showing extremely to very thin nexine and greatly reduced and much disorganized sexine, $\times 18,000$.



FIGURES 22–24. TEM exine sections of *Compsonura sprucei* (A. DC.) Warburg (J. D. Smith 5256, P-1948).—22. Whole grain exine section, showing aperture at top, $\times 3,500$.—23. Nonapertural exine section, showing average, essentially solid nexine, average to moderately thick columellate interstitium, and average tectum, $\times 18,000$.—24. Apertural exine section, showing extremely to very thin nexine and greatly reduced and much disorganized sexine, $\times 13,000$.

D. Smith 5256 (K), P-1948 (SEM, SEM-X, TEM); *Gentle* 2640 (K), P-1949. *C. ulei* Warburg, *Prance et al.* 8562 (GH), P-1136, (K), P-1954 (SEM, SEM-X); *Prance et al.* 8979 (K), P-1955.

Virola Aubl. (Figs. 25–96)

Pollen.—Apertures sulcate and generally sharply delimited externally, sometimes more or less sulcoidate and less evident externally. Shape usually boat-shaped, less commonly more or less globose-spherical, sometimes rectangular or triangular in outline with a straight apertural face and a markedly convex non-

apertural face. Polarity heteropolar. Symmetry usually bilateral, less commonly isobilateral. Size medium-sized to small (mean 27 μm , range 22–35 μm). Pollen-Unit monads. Exine Sculpturing reticuloid to reticulate, sometimes with banded, beaded, or granulate-beaded muri and occasionally with evident, free-standing columellae visible through the lumina of the reticulum. Exine Structure columellate (columellae frequently weakly attached to the nexine), tectate-perforate to semitectate; nonapertural exine about 1.35 μm thick, with a generally very thin (about 13% of total exine thickness on the average), although sometimes extremely thin or moderately thin, partially finely lamellate or essentially solid nexine, a moderately thick (about 46% of total exine thickness on the average) interstitium, and an average to moderately thick (about 41% of total exine thickness on the average) tectum, sexine usually with conspicuous, small, spherical, intra-exinous cavities; apertural exine with an extremely to very thin nexine and a reduced and much disorganized sexine. Exine Stratification wholly ectexinous; endexine none.

Specimens Examined.—*Virola albidiflora* Ducke, Schultes & Cabrera 13974 (A), P-1152; Forero et al. 6370 (S), P-2716; Krukoff 8103 (S), P-2717. *V. calophylla* Warburg, Krukoff 4713 (A), P-914,

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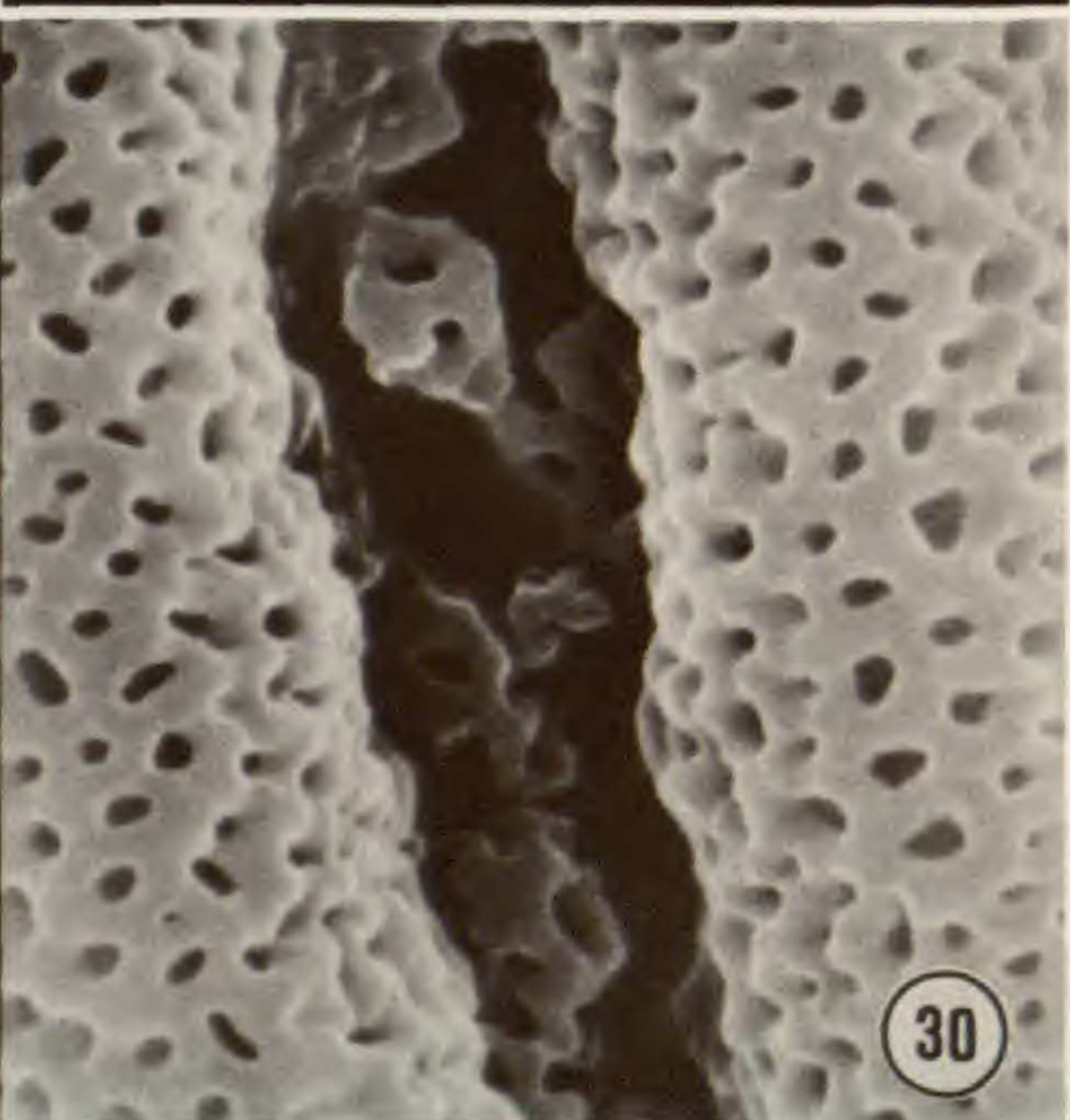
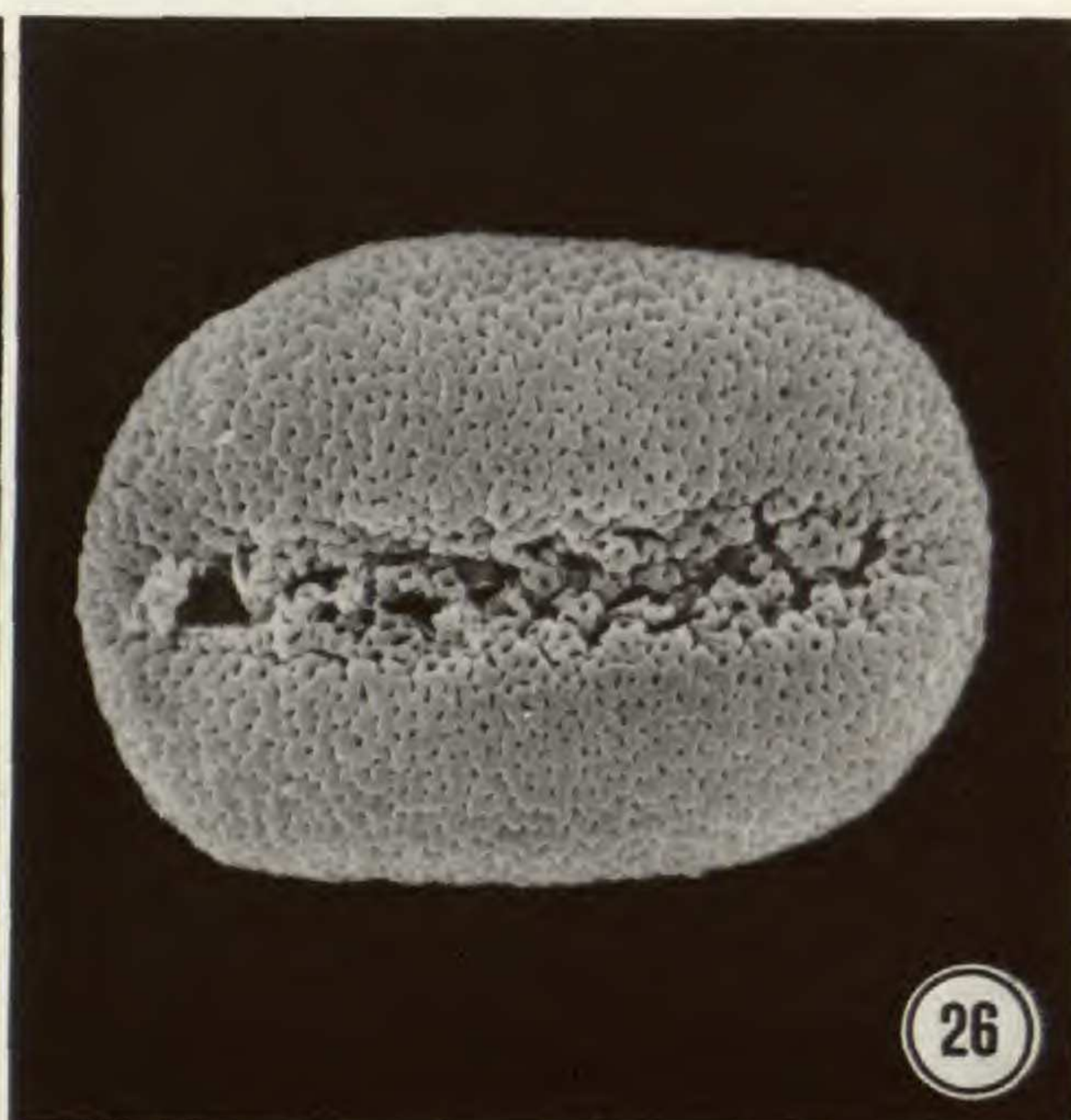
FIGURES 25–30. Whole pollen grains and apertural surface views of Type I pollen of *Virola* Aubl.—25. *V. calophylla* Warburg (Krukoff 4713, P-1995); $\times 2,200$.—26. *V. elongata* (Benth.) Warburg (Prance et al. 14081, P-2010); $\times 2,500$.—27, 29. *V. cuspidata* (Benth.) Warburg (27, Ducke 24467, P-1991; 29, Prance et al. 15120, P-1990), 29, apertural surface view; 27, $\times 2,000$, 29, $\times 15,000$.—28, 30. *V. duckei* A. C. Smith (28, Wurdack 2259, P-2719; 30, Froes 21248, P-1999), 30, apertural surface view; 28, $\times 3,000$, 30, $\times 8,000$.

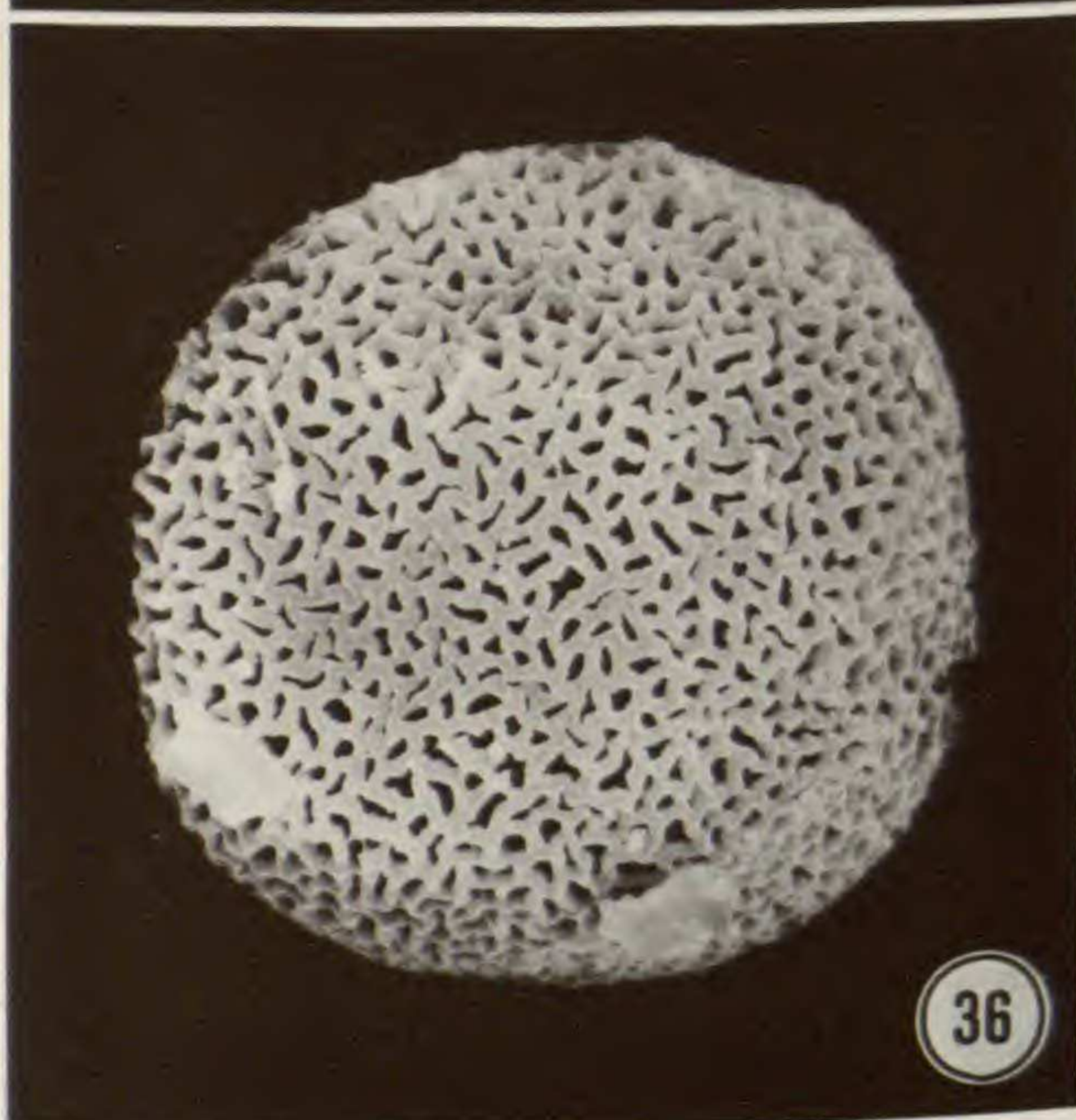
FIGURES 31–36. Whole pollen grains of Type II pollen of *Virola* Aubl.—31. *V. minutiflora* Ducke (Ducke 251, P-2726); $\times 3,400$.—32. *V. weberbaueri* Markgraf (Tessmann 4339, P-2734); $\times 2,800$.—33. *V. malmei* A. C. Smith (Malme 2033b, P-2724); $\times 2,200$.—34. *V. surinamensis* (Rol.) Warburg (*Plantae Surinamenses* 700, P-2002); $\times 2,000$.—35. *V. calophylloidea* Markgraf (Maguire et al. 56666, P-1997); $\times 2,800$.—36. *V. multinervia* Ducke (Maas et al. P12796, P-2728); $\times 2,000$.

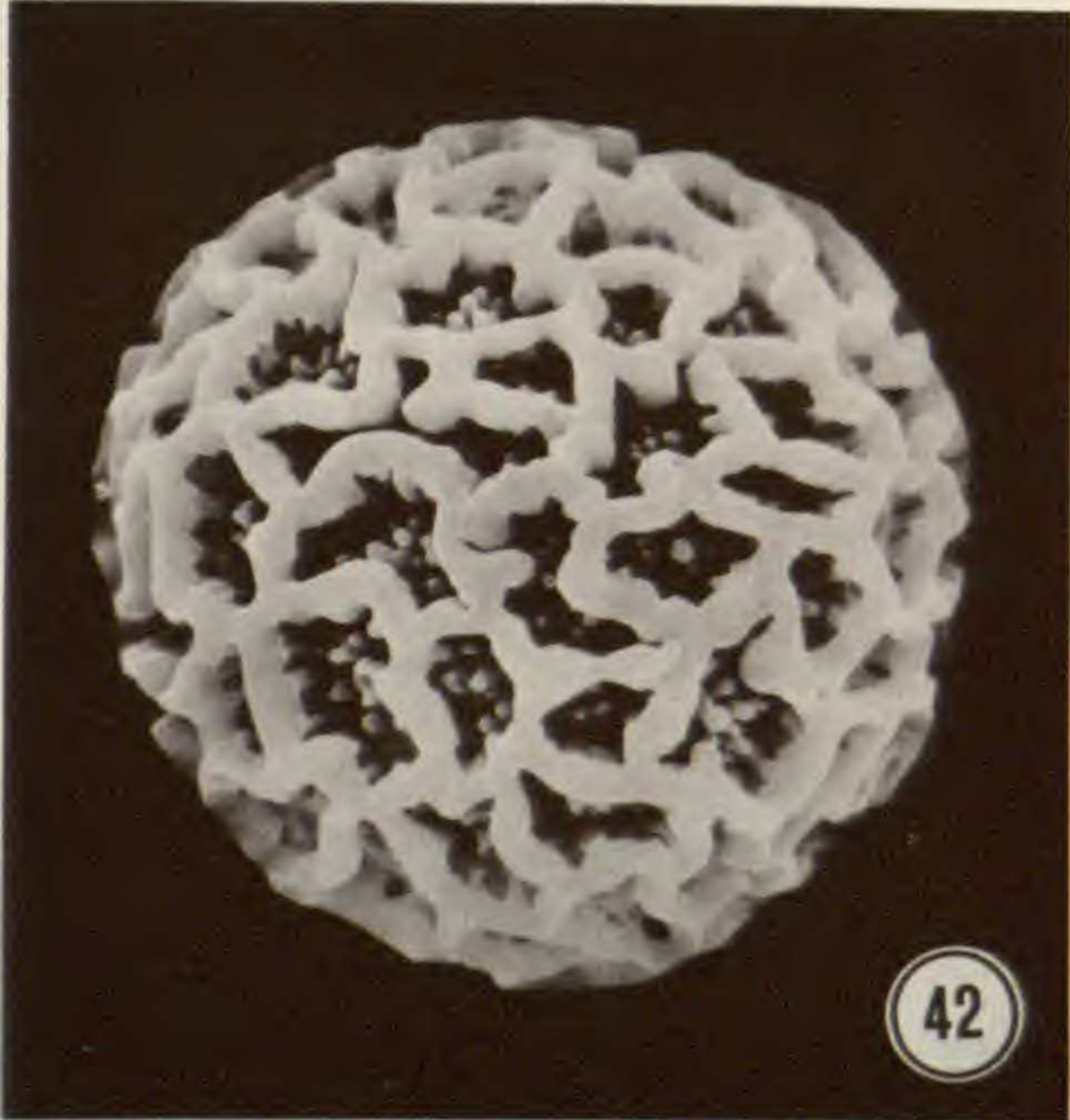
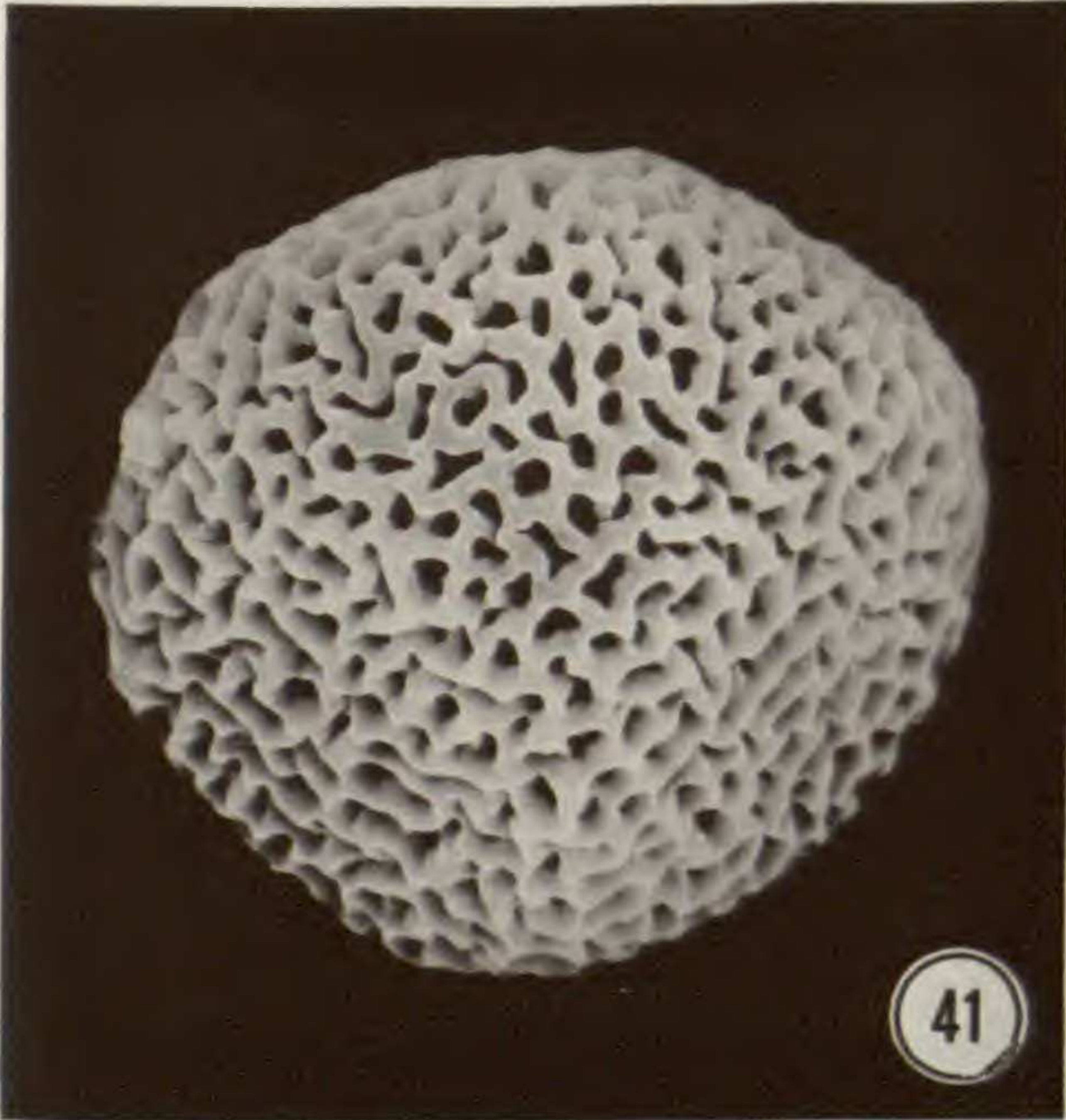
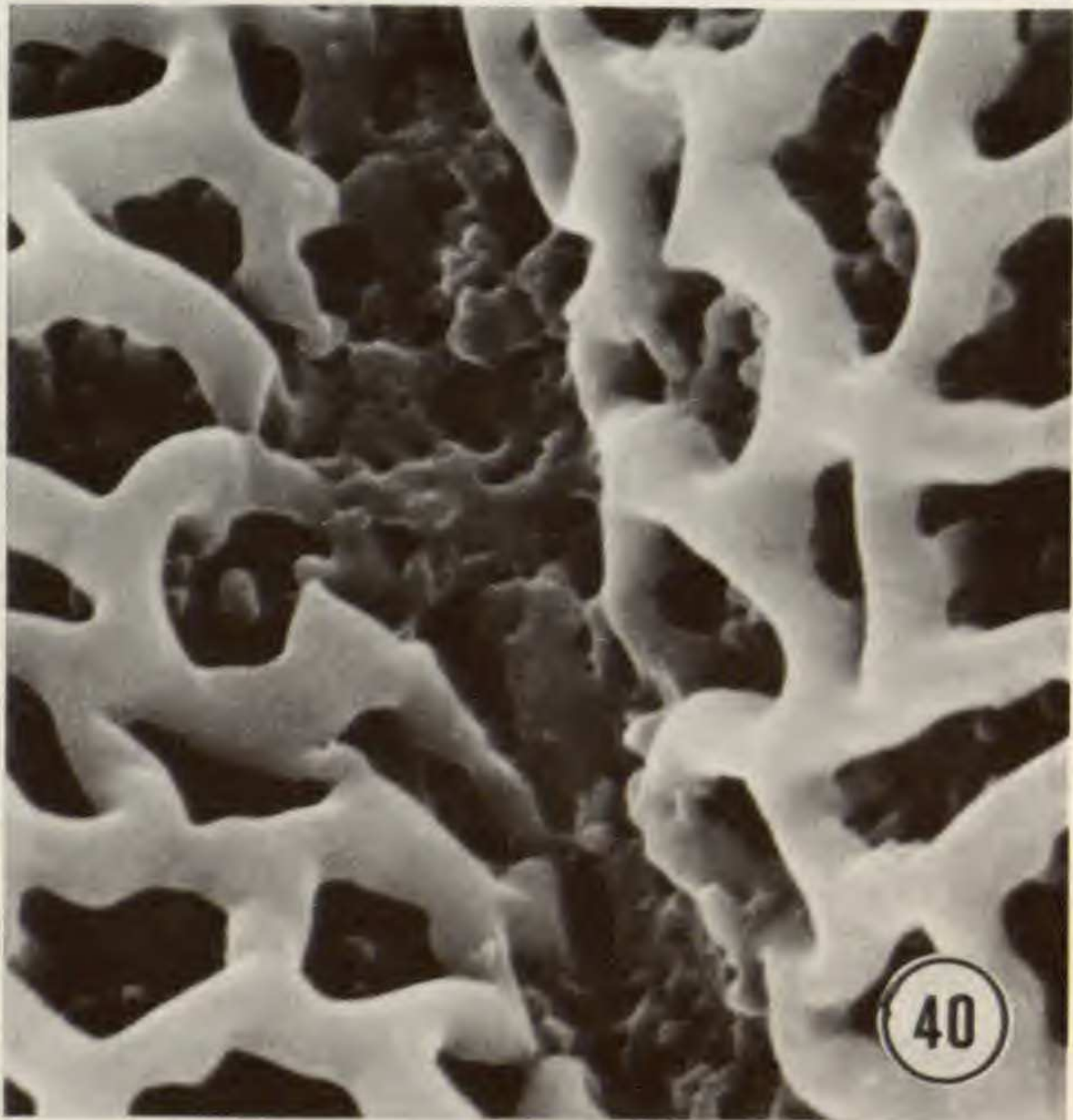
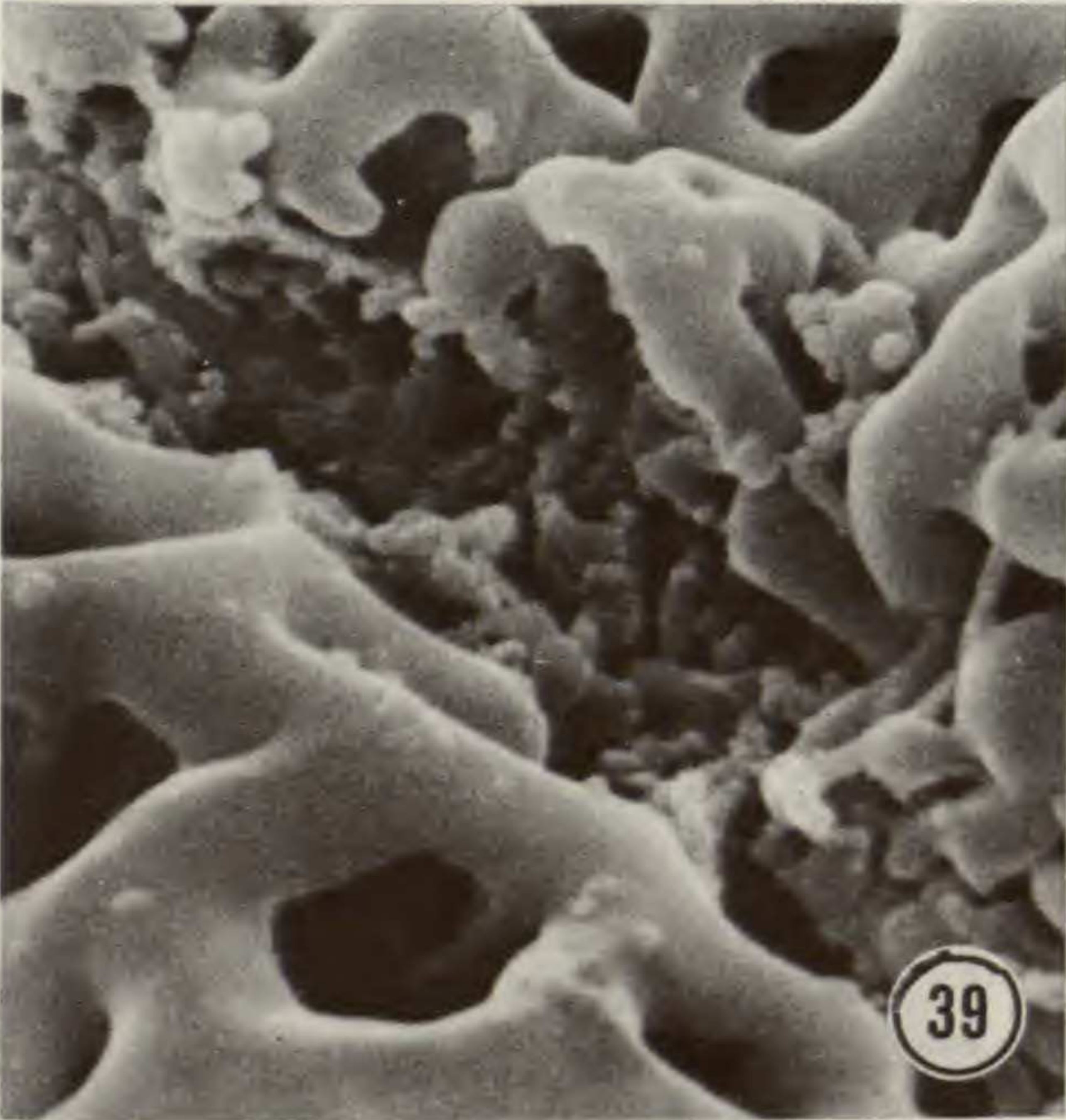
FIGURES 37–42. Whole pollen grains and apertural surface views of Type III pollen of *Virola* Aubl.—37, 39. *V. koschnyi* Warburg (Peck 373, P-1985), 39, apertural surface view; 37, $\times 2,200$, 39, $\times 16,000$.—38, 40. *V. multiflora* (Standl.) A. C. Smith (38, Schipp 858, P-1149; 40, Schipp 279, P-1986), 40, apertural surface view; 38, $\times 1,800$, 40, $\times 7,000$.—41. *V. melinonii* (Benoist) A. C. Smith (Pires et al. 50526, P-2725); $\times 2,000$.—42. *V. venosa* (Benth.) Warburg (Pires et al. 50550, P-2005), note the numerous free-standing columellae visible through lumina of the reticulum; $\times 2,000$.

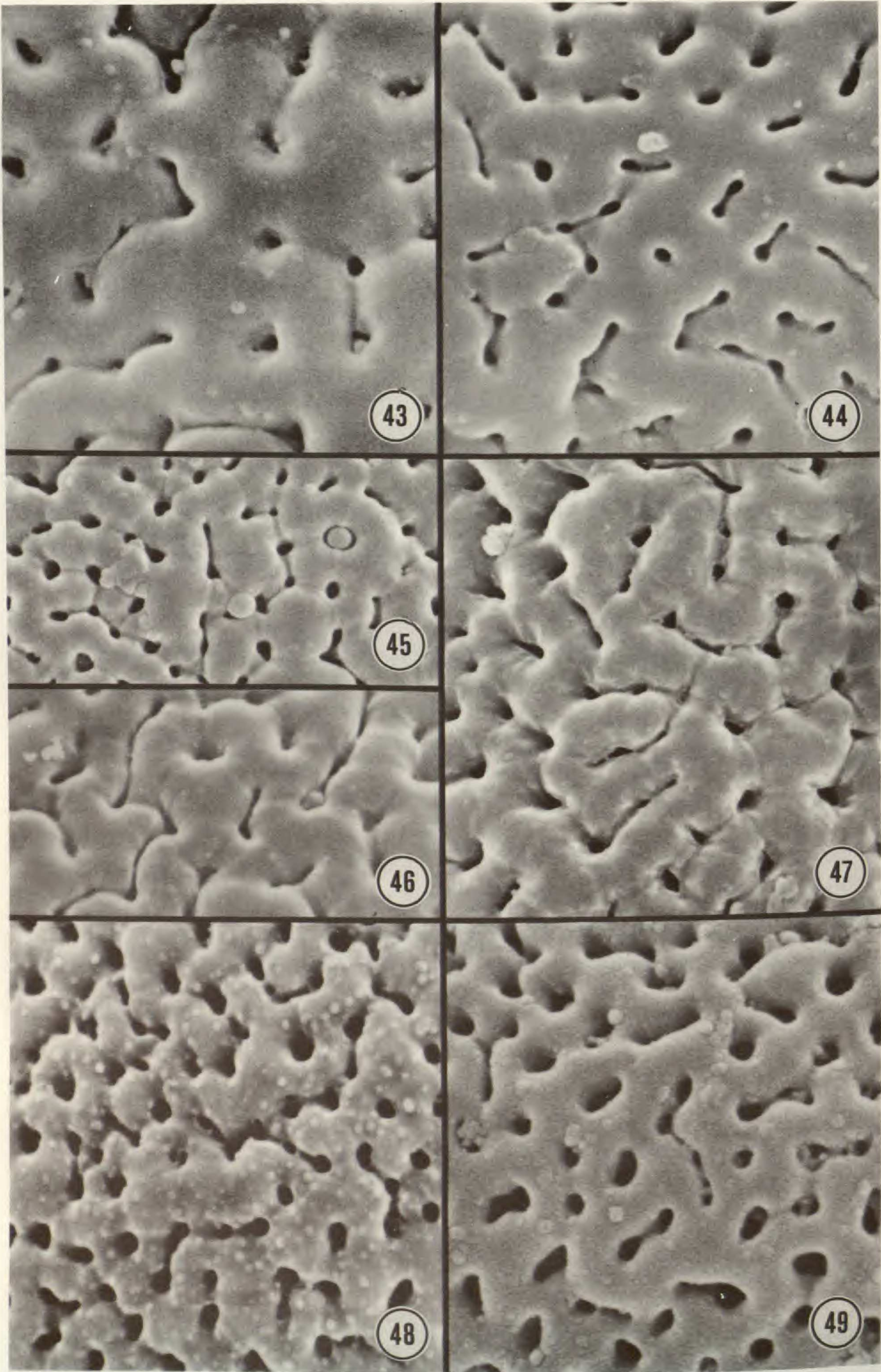
FIGURES 43–49. Exine surface of Type I pollen of *Virola* Aubl.—43. *V. calophylla* Warburg (Krukoff 4713, P-1995); $\times 16,000$.—44. *V. macrocarpa* A. C. Smith (Cuatrecasas 17540, P-1158); $\times 16,000$.—45. *V. peruviana* (A. DC.) Warburg (Schultes 6031, P-2013); $\times 12,000$.—46. *V. mollissima* (A. DC.) Warburg (Klug 3128, P-913); $\times 12,000$.—47. *V. elongata* (Benth.) Warburg (Prance et al. 14081, P-2010); $\times 16,000$.—48. *V. lorentensis* A. C. Smith (Klug 2822, P-2012); $\times 12,000$.—49. *V. duckei* A. C. Smith (Wurdack 2259, P-2719); $\times 16,000$.

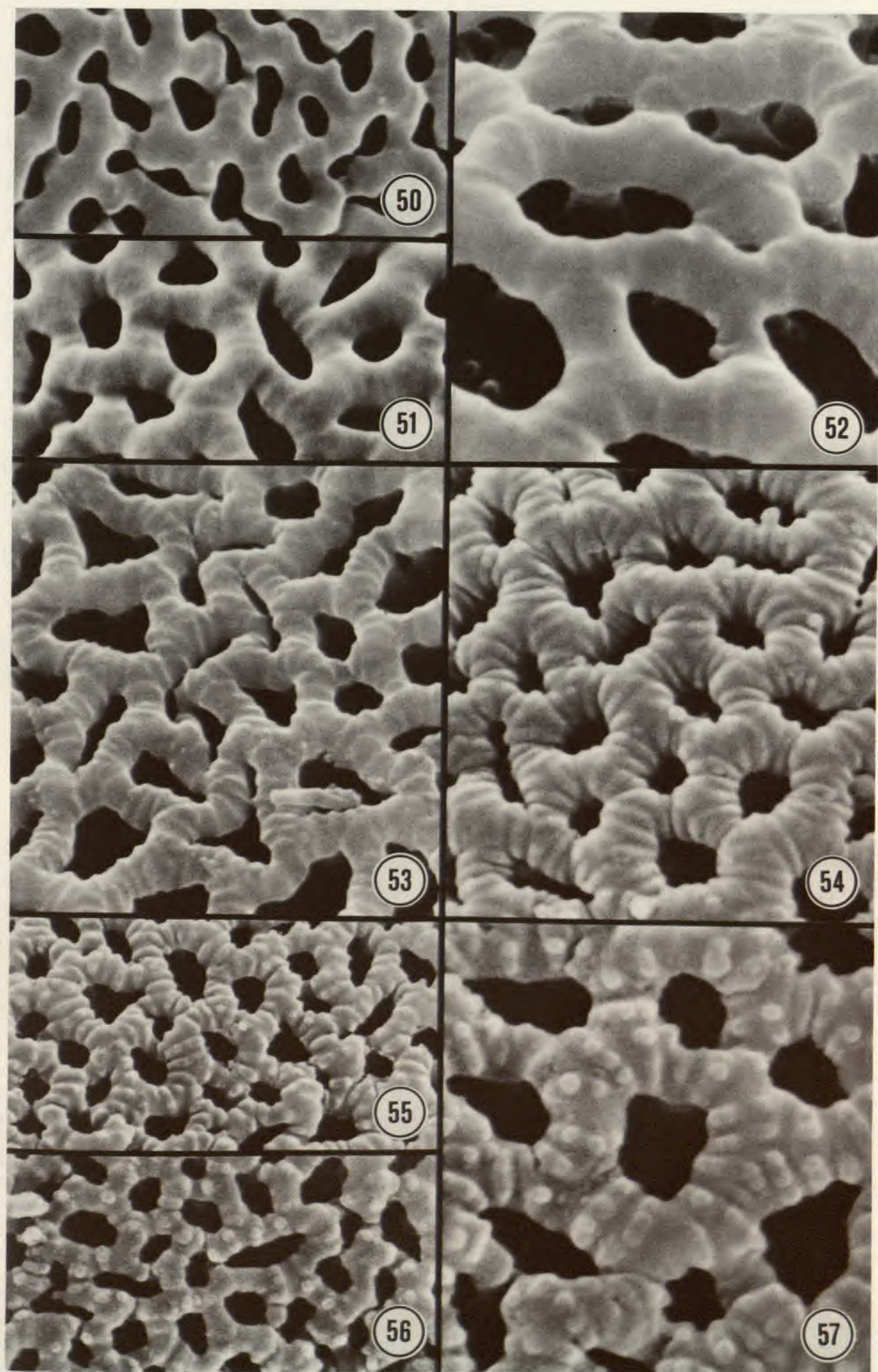
FIGURES 50–57. Exine surface of Type II pollen of *Virola* Aubl.—50. *V. glaziovii* Warburg (Maguire et al. 56267, P-2003), note very faintly banded muri; $\times 12,000$.—51. *V. malmei* A. C. Smith (Malme 2033b, P-2724), note faintly banded muri; $\times 12,000$.—52. *V. carinata* (Benth.) Warburg (Ule 7988; P-2007), note faintly banded muri; $\times 24,000$.—53. *V. multinervia* Ducke (Maas et al. P12796, P-2728), note banded muri; $\times 16,000$.—54. *V. calophylloidea* Markgraf (Maguire et al. 56666, P-1997), note distinctly banded muri; $\times 16,000$.—55, 57. *V. weberbaueri* Markgraf (Tessmann 4339, P-2734), note coarsely granulate-banded muri; 55, $\times 12,000$, 57, $\times 24,000$.—56. *V. pavonis* (A. DC.) A. C. Smith (Ducke 259, P-1160), note coarsely granulate-banded muri; $\times 12,000$.











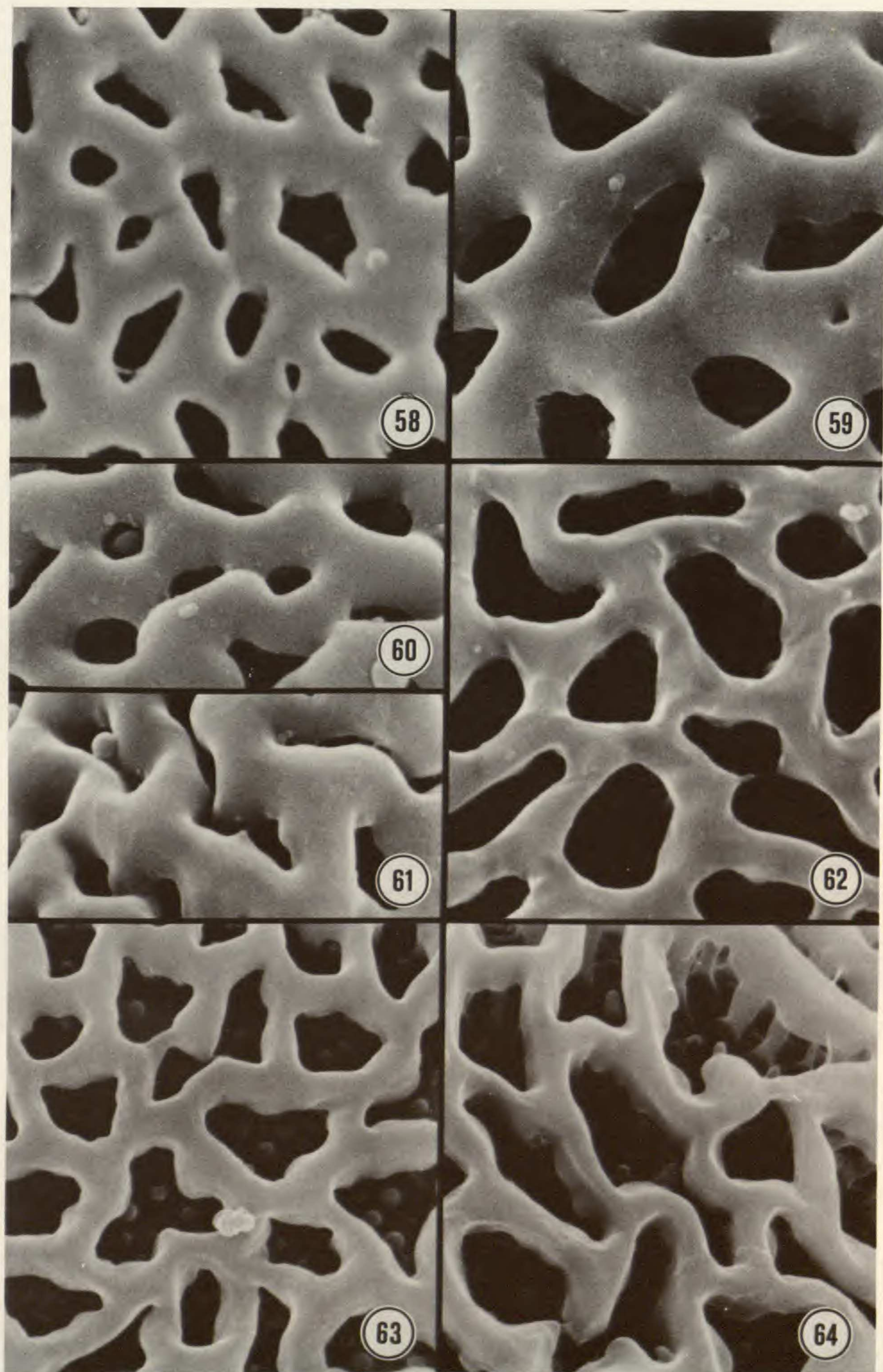
(K), P-1995 (SEM); *Froes* 21222 (K), P-1994 (SEM). *V. calophylloidea* Markgraf, *Ducke* 20 (A), P-1153, (S), P-2718; *Maguire et al.* 56666 (K), P-1997 (SEM). *V. carinata* (Benth.) Warburg, *Froes* 21172 (GH), P-912; *Ule* 7988 (K), P-2007 (SEM, TEM); *Schultes & Black* 8352 (K), P-2015 (SEM, TEM). *V. cuspidata* (Benth.) Warburg, *Ducke* 254 (A), P-909; *Prance et al.* 15120 (K), P-1990 (SEM); *Ducke* 24467 (K), P-1991 (SEM). *V. divergens* Ducke, *Krukoff* 1120 (A), P-1154 (SEM), (K), P-1987 (SEM, SEM-X, TEM); *Ducke* 174 (K), P-1988. *V. duckei* A. C. Smith, *Froes* 21248 (K), P-1999 (SEM); *Wurdack* 2259 (S), P-2719 (SEM). *V. elongata* (Benth.) Warburg, *Prance et al.* 3259 (GH), P-1156; *Klug* 2944 (A), P-1164; A. C. Smith 2524 (K), P-1993 (SEM); *Prance et al.* 14081 (K), P-2010 (SEM, SEM-X, TEM). *V. flexuosa* A. C. Smith, *Tessmann* 3207 (S), P-2720 (SEM, TEM). *V. gardneri* (A. DC.) Warburg, *Ducke* 25105 (S), P-2721. *V. glaziovii* Warburg, *Maguire et al.* 56267 (K), P-2003 (SEM, SEM-X). *V. guatemalensis* (Hemsl.) Warburg, *Steyermark* 47624 (A), P-1148 (SEM). *V. koschnyi* Warburg, *Skutch* 4260 (A), P-908 (SEM), (S), P-2722; *Peck* 373 (K), P-1985 (SEM, SEM-X, TEM). *V. loretensis* A. C. Smith, *Klug* 2822 (K), P-2012 (SEM, TEM). *V. macrocarpa* A. C. Smith, *Cuatrecasas* 17540 (A), P-1158 (SEM, TEM). *V. malmei* A. C. Smith, *Malme* 2033b (S), P-2724 (SEM). *V. melinonii* (Benoist) A. C. Smith, *Ducke* 1268 (A), P-1159; *Pires et al.* 50526 (S), P-2725 (SEM). *V. minutiflora* Ducke, *Ducke* 251 (S), P-2726 (SEM). *V. mollissima* (A. DC.) Warburg, *Klug* 3128 (A), P-913 (SEM), (S), P-2727 (SEM, SEM-X). *V. multiflora* (Standl.) A. C. Smith, *Schipp* 858 (GH), P-1149 (SEM); *Schipp* 279 (K), P-1986 (SEM, TEM). *V. multinervia* Ducke, *Ducke* 24556 (K), P-1998; *Maas et al.* P12796 (S), P-2728 (SEM). *V. nobilis* A. C. Smith, *Allen* 5774 (GH), P-1150 (SEM). *V. officinalis* Warburg, *Martius* 183 (L), P-2831 (SEM). *V. oleifera* (Schott) A. C. Smith, *Glaziou* 12140 (K), P-2000 (SEM, SEM-X). *V. pavonis* (A. DC.) A. C. Smith, *Ducke* 259 (A), P-1160 (SEM); *Ruiz* 61 (K), P-2014 (SEM); *Klug* 3085 (K), P-2016. *V. peruviana* (A. DC.) Warburg, *Wurdack* 2272 (GH), P-1161; *Ducke* 24552 (K), P-1996 (SEM); *Schultes* 6031 (K), P-2013 (SEM, SEM-X, TEM). *V. sebifera* Aubl., *Skutch* 3118 (A), P-1151 (SEM), (K), P-1984; *Krukoff* 11644 (K), P-1989 (SEM). *V. sessilis* (A. DC.) Warburg, *Malme* 2007c (S), P-2729 (SEM, TEM); *Malme* 2007b (S), P-2730 (SEM, TEM). *V. subsessilis* (Benth.) Warburg, *Irwin et al.* 21508 (GH), P-1163; *Prance & Silva* 58503 (S), P-2732 (SEM). *V. surinamensis* (Rol.) Warburg, *Eggers s.n.* (GH) P-910; *Sandwith* 477 (K), P-2001; *Plantae Surinamenses* 700 (K), P-2002 (SEM). *V. venosa* (Benth.) Warburg, *Herb. Acad. Rhenotraiect*, *Arbor* No. 1336 (A), P-1165; *Pires et al.* 50550 (K), P-2005 (SEM); *Prance et al.* 6749 (S), P-2733. *V. weberbaueri* Markgraf, *Tessmann* 4339 (S), P-2734 (SEM, SEM-X, TEM).

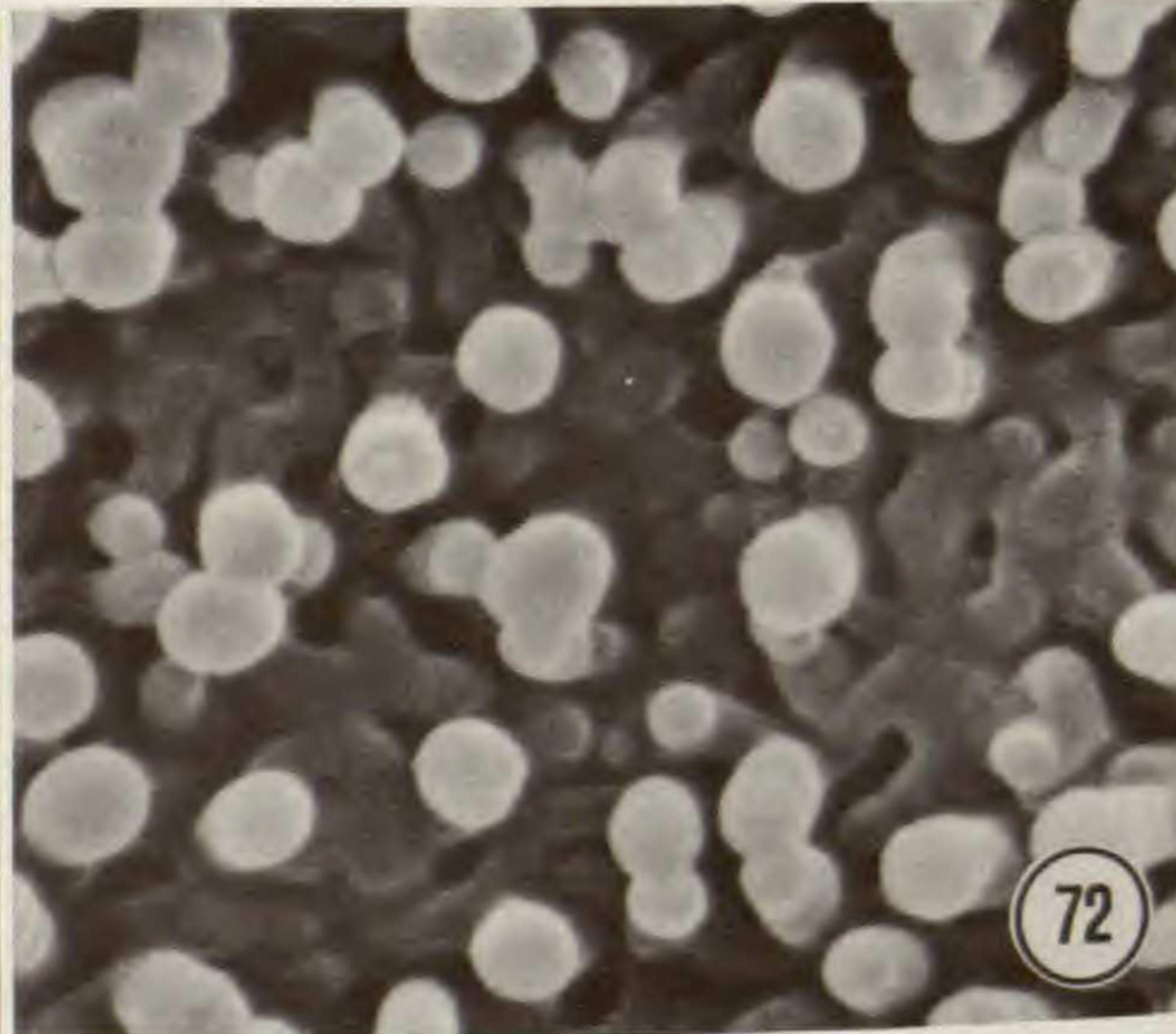
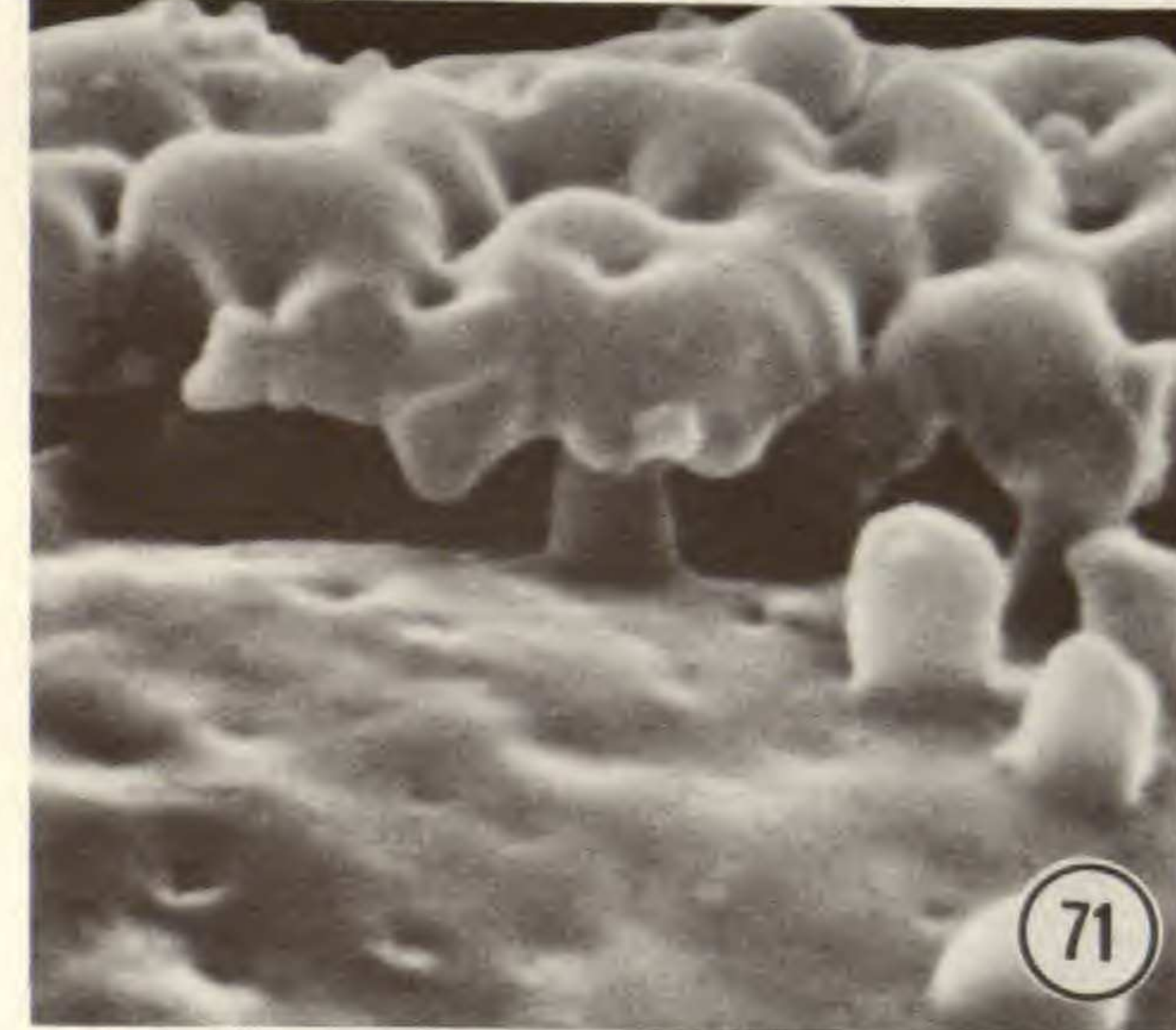
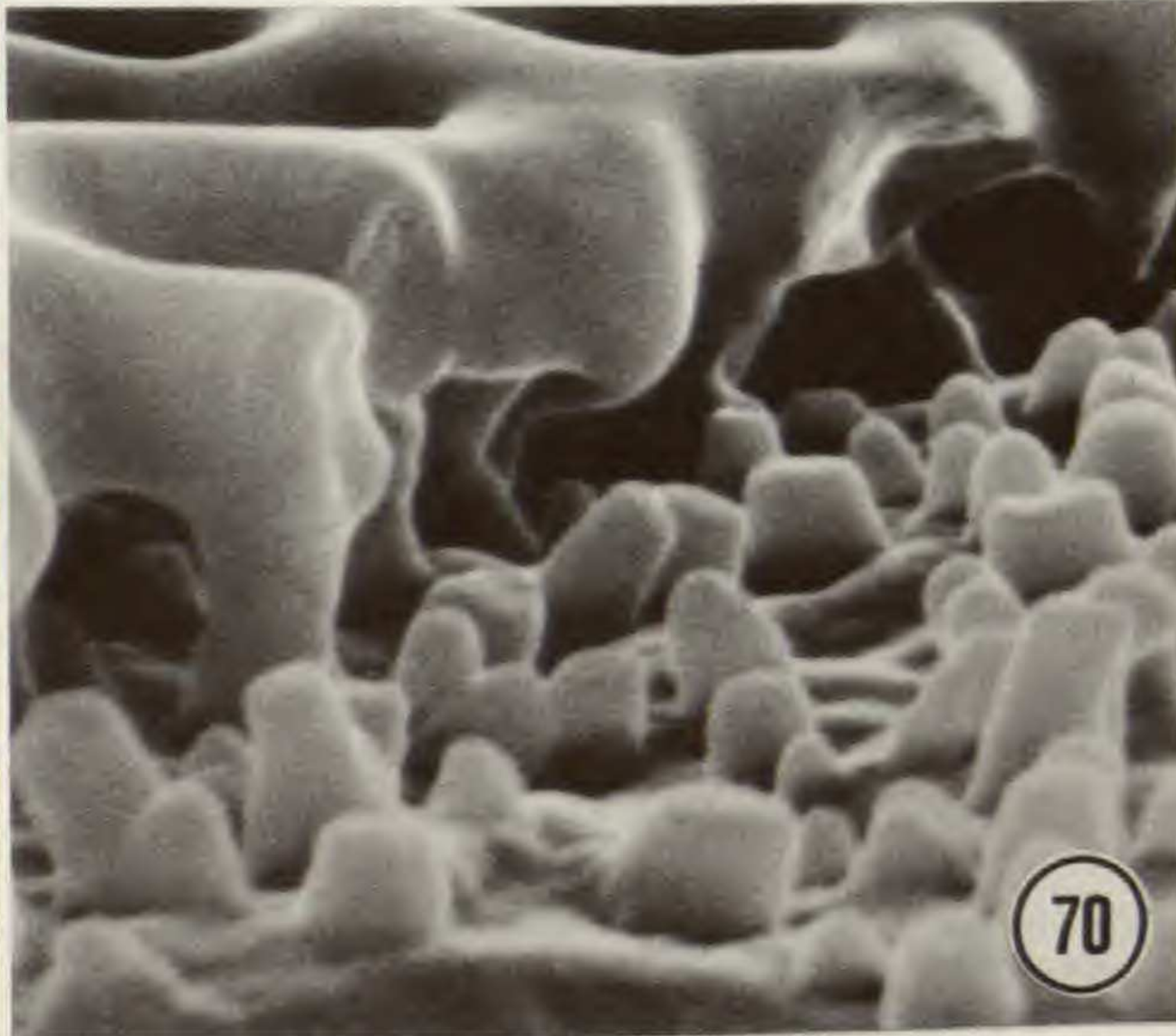
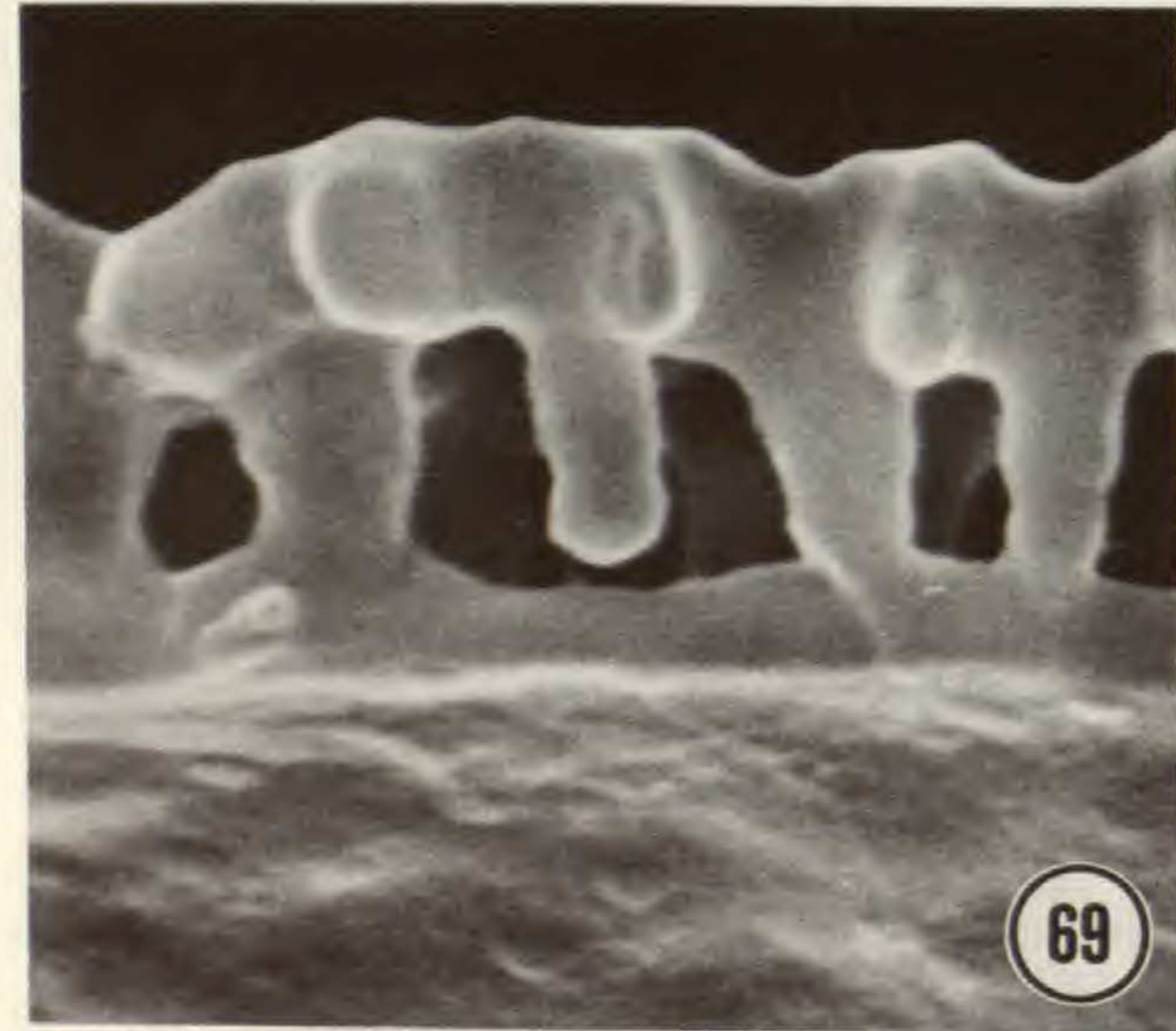
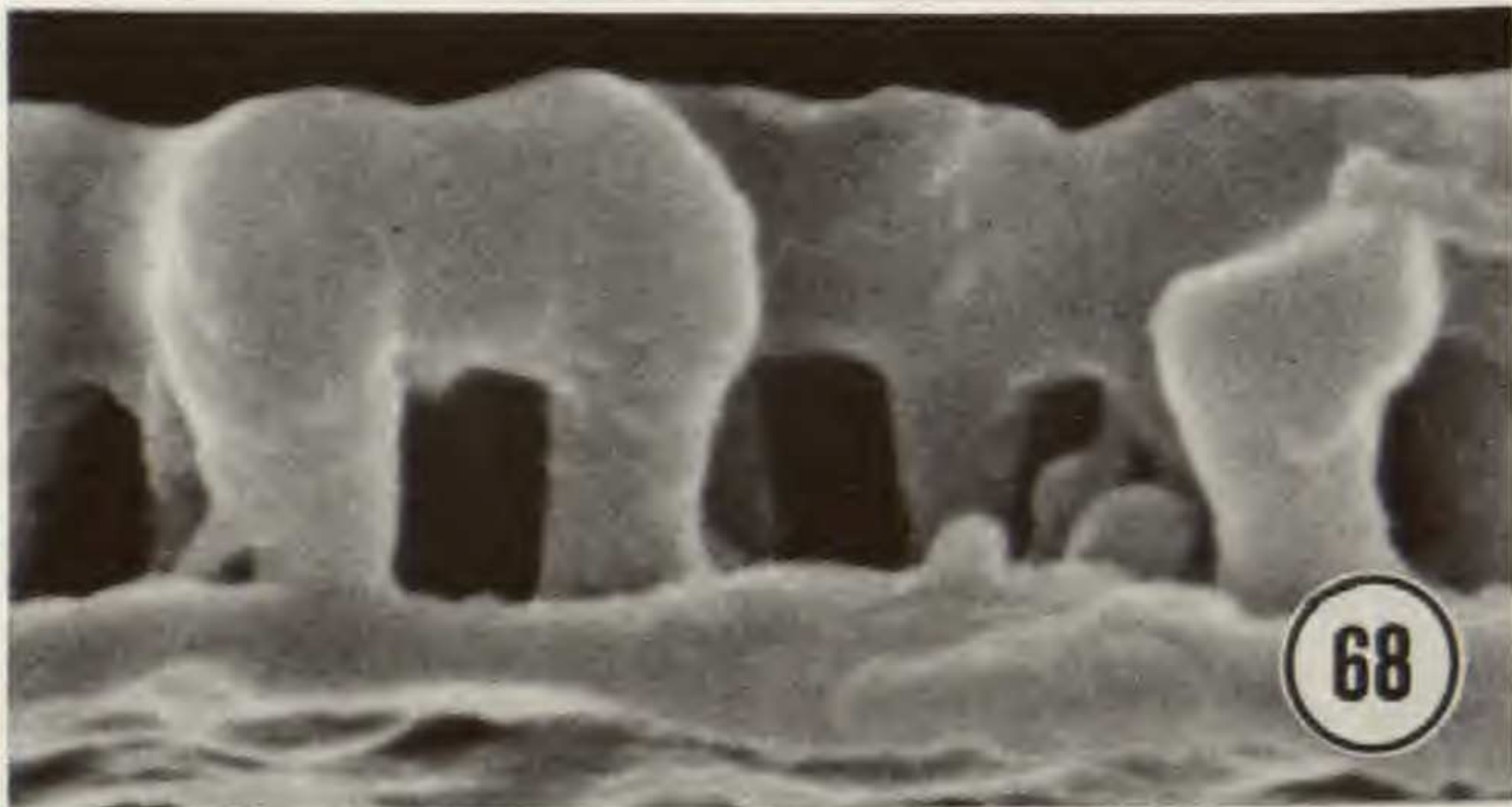
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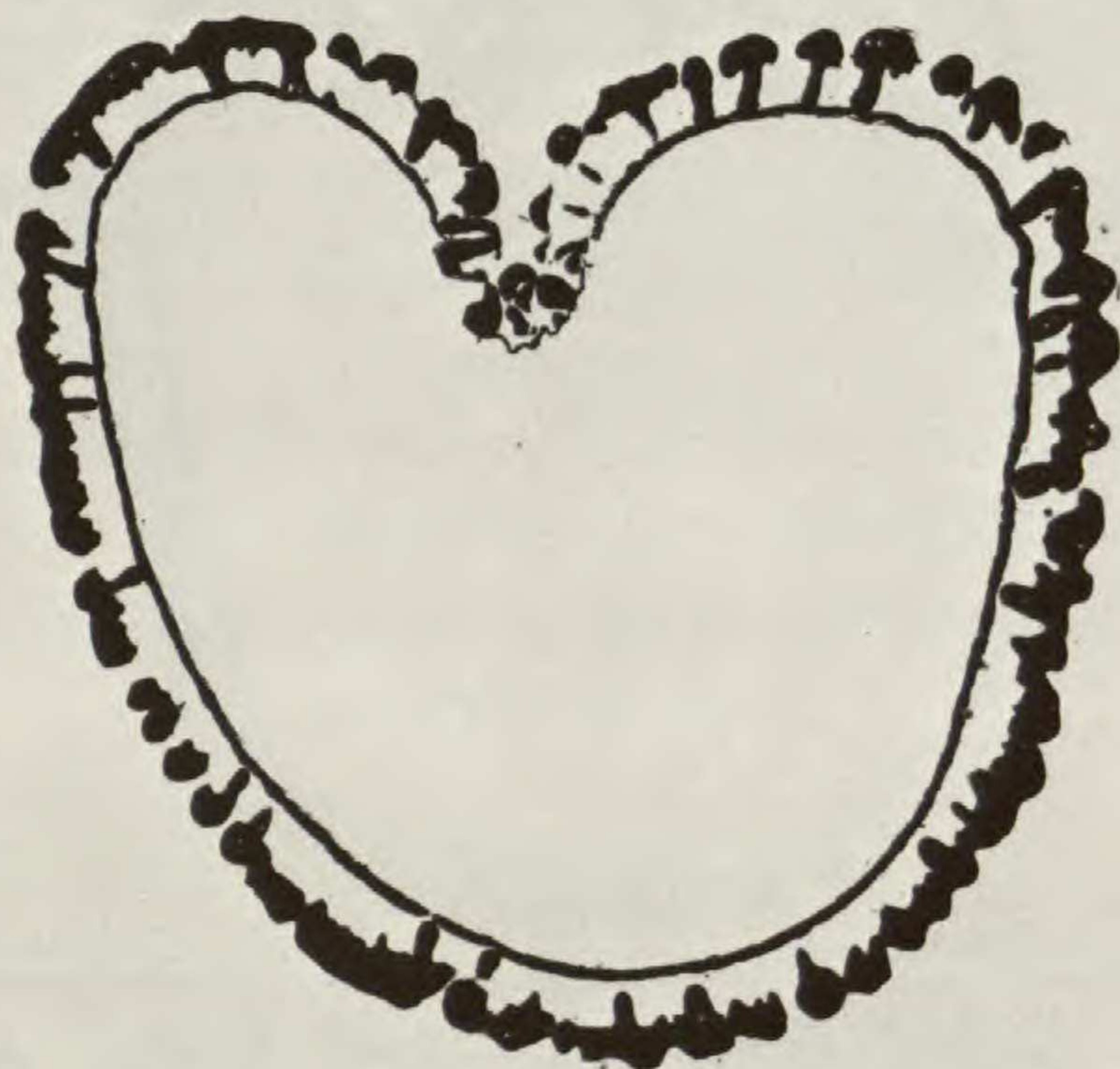
FIGURES 58–64. Exine surface of Type III pollen of *Virola* Aubl.—58. *V. sessilis* (A. DC.) Warburg (*Malme* 2007b, P-2730); $\times 16,000$.—59. *V. subsessilis* (Benth.) Warburg (*Prance & Silva* 58503, P-2732); $\times 16,000$.—60. *V. melinonii* (Benoist) A. C. Smith (*Pires et al.* 50526, P-2725); $\times 12,000$.—61. *V. officinalis* Warburg (*Martius* 183, P-2831); $\times 12,000$.—62. *V. oleifera* (Schott) A. C. Smith (*Glaziou* 12140, P-2000); $\times 12,000$.—63. *V. multiflora* (Standl.) A. C. Smith (*Schipp* 279, P-1986), note free-standing columellae; $\times 8,000$.—64. *V. venosa* (Benth.) Warburg, (*Pires et al.* 50550, P-2005), note free-standing columellae; $\times 8,000$.

FIGURES 65–72. SEM nonapertural exine sections of *Virola* Aubl.—65. *V. mollissima* (A. DC.) Warburg (*Klug* 3128, P-2727).—66. *V. elongata* (Benth.) Warburg (*Prance et al.* 14081, P-2010), note rounded end of columella to left and granular inner surface of tectum.—67, 72. *V. peruviana* (A. DC.) Warburg (*Schultes* 6031, P-2013), 67, note granular inner surface of tectum, 72, tangential section through interstitium looking at inner surface of tectum.—68. *V. oleifera* (Schott) A. C. Smith (*Glaziou* 12140, P-2000).—69. *V. glaziovii* Warburg (*Maguire et al.* 56267, P-2003), note inner surface of nexine at bottom and columella pendulous from inner surface of tectum in the center.—70. *V. koschnyi* Warburg (*Peck* 373, P-1985), partial tangential section through middle of interstitium.—71. *V. divergens* Ducke (*Krukoff* 1120, P-1987), note circular depressions left in surface of nexine by separation of weakly attached columellae. All $\times 16,000$ except Fig. 69, which is $\times 24,000$.

FIGURES 73–77. TEM exine sections of *Virola divergens* Ducke (*Krukoff* 1120, P-1987).—73. Whole grain exine section, showing aperture at top, $\times 5,000$.—74, 76. Nonapertural exine sections, showing very thin, partially finely lamellate nexine, moderately thick columellate interstitium, and average to moderately thick tectum; note conspicuous, small, spherical, intra-exinous cavities in sexine; 74, $\times 16,000$, 76, $\times 18,000$.—75. Apertural exine section, showing extremely thin nexine and reduced and much disorganized sexine, $\times 19,000$.—77. Nonapertural exine, tangential section through tectum, showing spherical, intra-exinous, sexinous cavities, $\times 16,000$.







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74



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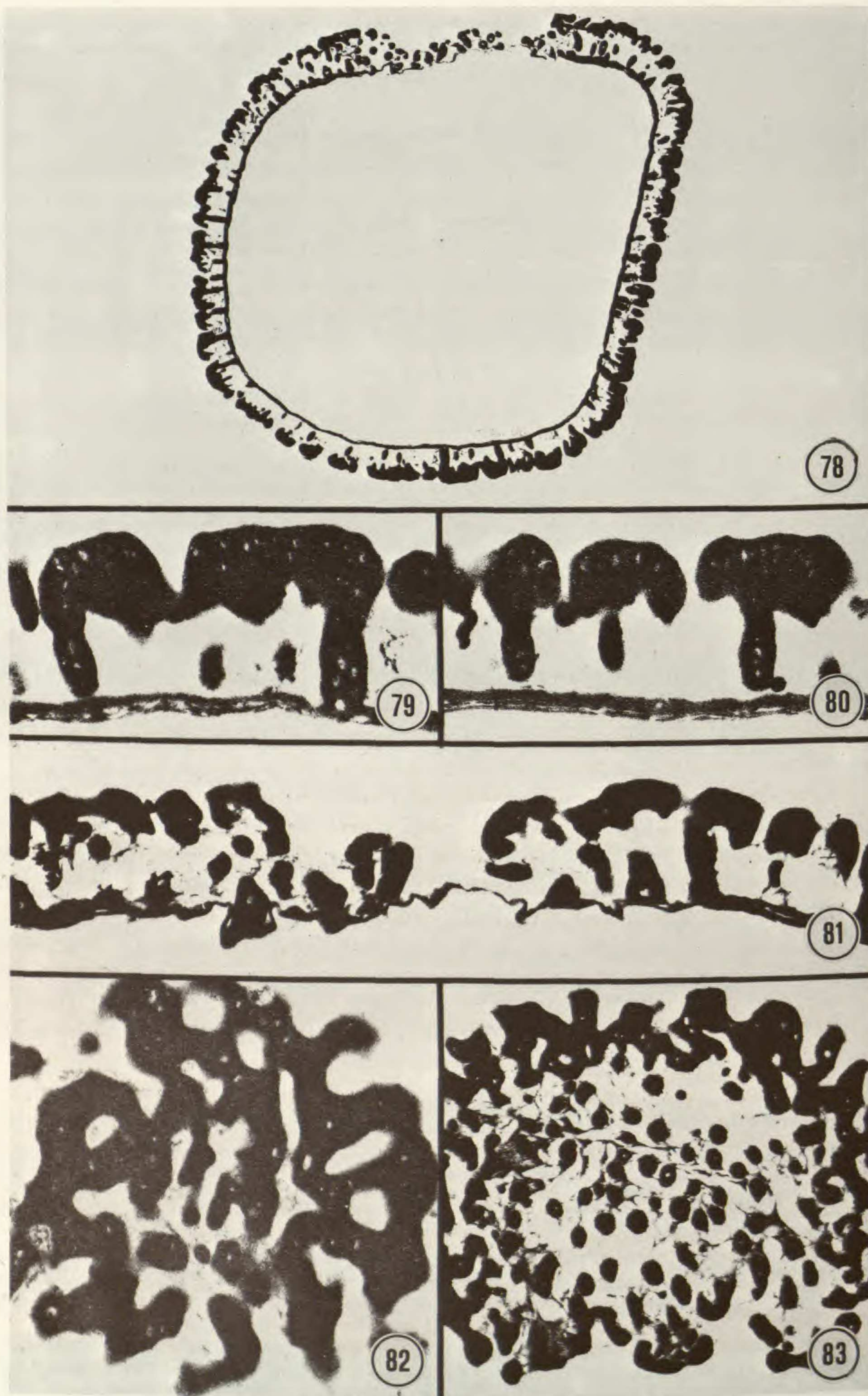


TABLE 1. Arrangement of *Virola* species according to pollen type.^a

Pollen Type I	
<i>V. calophylla</i> (3)	<i>V. loretensis</i> (1)
<i>V. cuspidata</i> (2)	<i>V. macrocarpa</i> (3)
<i>V. divergens</i> (1)	<i>V. mollissima</i> (1)
<i>V. duckei</i> (4)	<i>V. peruviana</i> (2)
<i>V. elongata</i> (2)	<i>V. sebifera</i> (2)
Pollen Type II	
<i>V. calophylloidea</i> (3)	<i>V. minutiflora</i> (4)
<i>V. carinata</i> (5)	<i>V. multinervia</i> (4)
<i>V. flexuosa</i> (4)	<i>V. pavonis</i> (5)
<i>V. glaziovii</i> (5)	<i>V. surinamensis</i> (5)
<i>V. malmei</i> (5)	<i>V. weberbaueri</i> (2)
Pollen Type III	
<i>V. guatemalensis</i> (5)	<i>V. officinalis</i> (4)
<i>V. koschnyi</i> (4)	<i>V. oleifera</i> (5)
<i>V. melinonii</i> (5)	<i>V. sessilis</i> (6)
<i>V. multiflora</i> (5)	<i>V. subsessilis</i> (6)
<i>V. nobilis</i> (5)	<i>V. venosa</i> (5)

^a Numbers in parentheses after each species refer to placement in species groups recognized by Smith (1938).

DISCUSSION

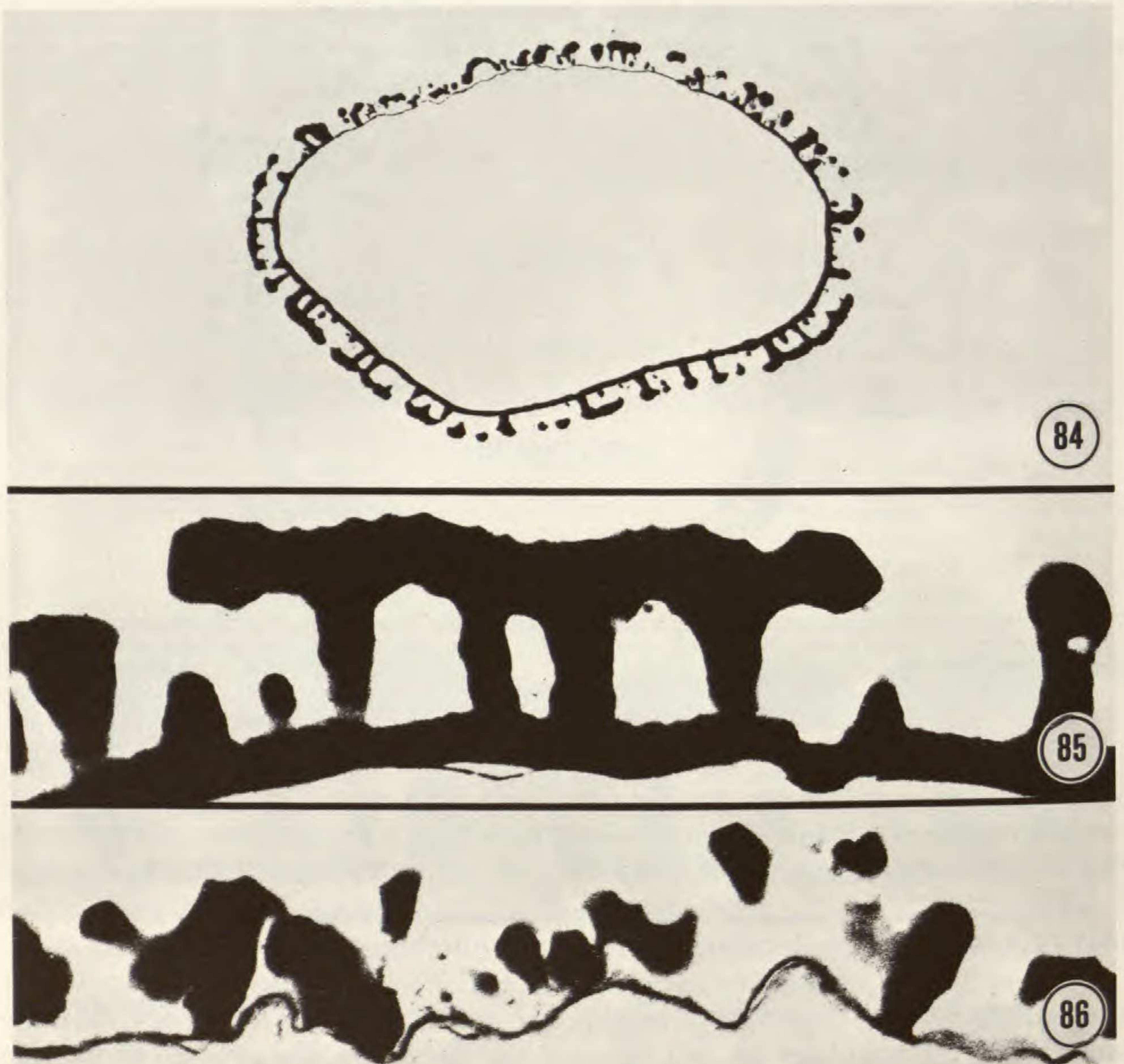
Apertures.—Pollen of *Compsonura* and *Virola* is usually sulcate (Figs. 1, 3–4, 25–28, 31–33, 37–38) with an aperture that is sharply defined externally (Figs. 1, 25–26, 29–30, 39–40), although sometimes, particularly in *Virola*, the pollen may be more or less sulcoidate with the aperture less evident externally.

Shape, Polarity, and Symmetry.—The pollen of the two genera studied is usually boat-shaped (Figs. 3, 37–38) although sometimes it is more or less globose-spherical (Figs. 5, 34–36, 41–42). Sometimes the pollen grains of both of these genera are more or less rectangular (Figs. 25–26, 28) or triangular in outline with a straight apertural face and a markedly convex nonapertural face (Fig. 27). The unusual triangular-rectangular shape of some mature myristicaceous pollen grains may be related to the unusual planar orientation of their sulcate apertures, as suggested by Kuprianova (1967) (cf. also Walker & Walker, in press, 3). Polarity of their pollen is always more or less heteropolar, while symmetry is generally bilateral.

Size.—Pollen grains of both genera are medium-sized to small. *Compsonura* pollen averages 24 μm and ranges from 21–27 μm , with the largest grains in *C.*

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FIGURES 78–83. TEM exine sections of *Virola peruviana* (A. DC.) Warburg (*Schultes* 6031, P-2013).—78. Whole grain exine section, showing aperture at top, $\times 4,000$.—79–80. Nonapertural exine section, showing very thin, finely lamellate nexine, moderately thick interstitium with pendulous columellae, and average to moderately thick tectum; note conspicuous, small, spherical, intra-exinous cavities in sexine, both $\times 20,000$.—81. Apertural exine section, showing extremely thin nexine and reduced and much disorganized sexine, $\times 14,000$.—82–83. Nonapertural exine tangential sections through tectum (82) and interstitium (83), showing spherical, intra-exinous, sexinous cavities; 82, $\times 19,000$, 83, $\times 13,000$.

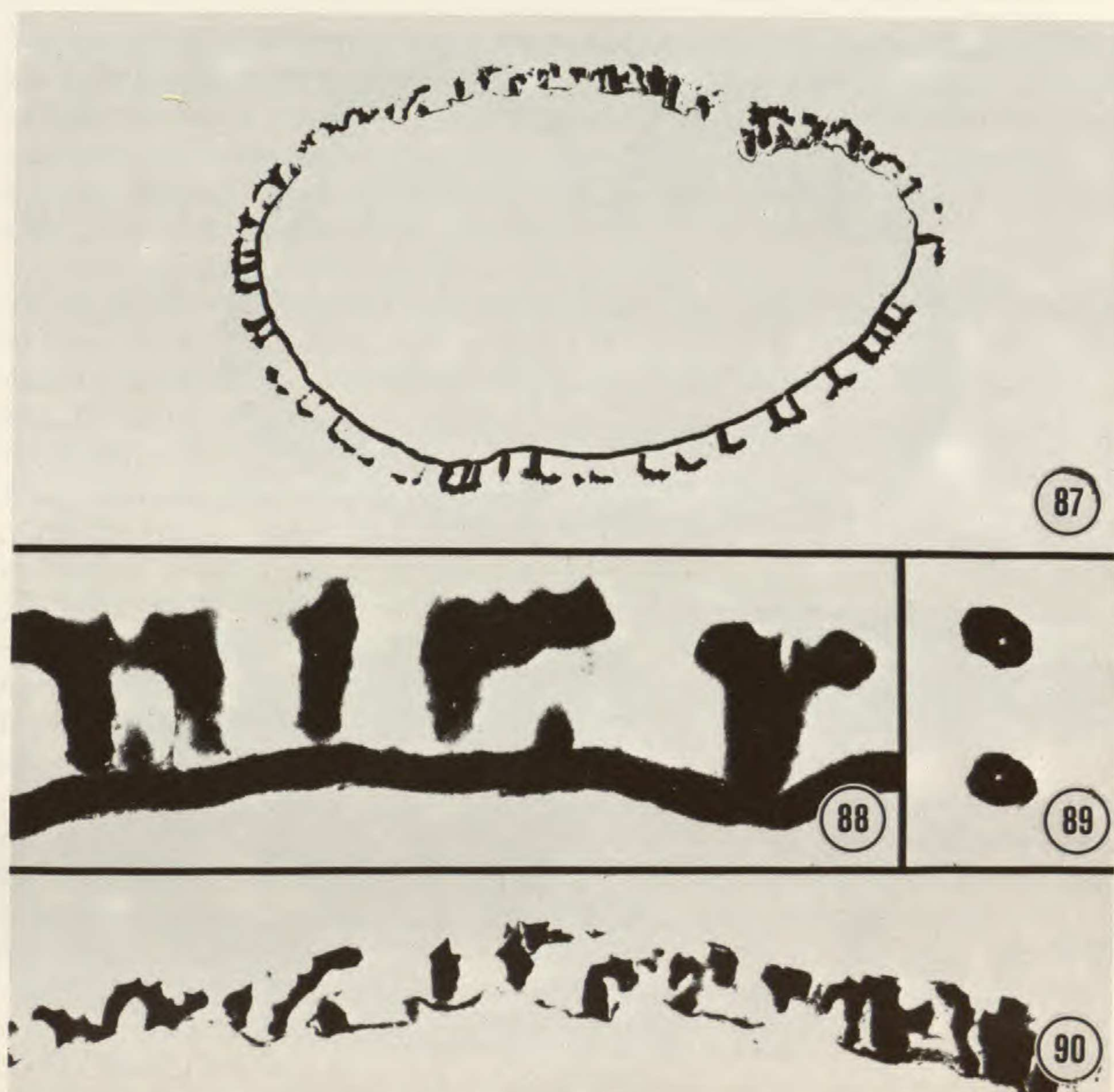


FIGURES 84–86. TEM exine sections of *Virola carinata* (Benth.) Warburg (Ule 7988, P-2007).—84. Whole grain exine section, showing aperture at top left, $\times 3,400$.—85. Nonapertural exine section, showing moderately thin, essentially solid nexine, moderately thick columellate interstitium, and average to moderately thick tectum, $\times 21,000$.—86. Apertural exine section, showing extremely thin nexine and reduced and much disorganized sexine, $\times 20,000$.

sprucei and the smallest in *C. mutisii*. *Compsonura* section *Compsonura* has slightly larger pollen on the average (with a mean for the section of $25\ \mu\text{m}$), while the pollen of *Compsonura* section *Coniostele* is slightly smaller on the average (with a mean for the section of $23\ \mu\text{m}$). Pollen of *Virola* averages $27\ \mu\text{m}$ and ranges from 22 – $35\ \mu\text{m}$, with the largest grains in *V. koschnyi* and *V. guatemalensis* and the smallest grains in *V. calophylloidea*.

Pollen-Unit.—Pollen of both *Compsonura* and *Virola* is shed as solitary grains or monads (Figs. 1–6, 25–28, 31–38, 41–42).

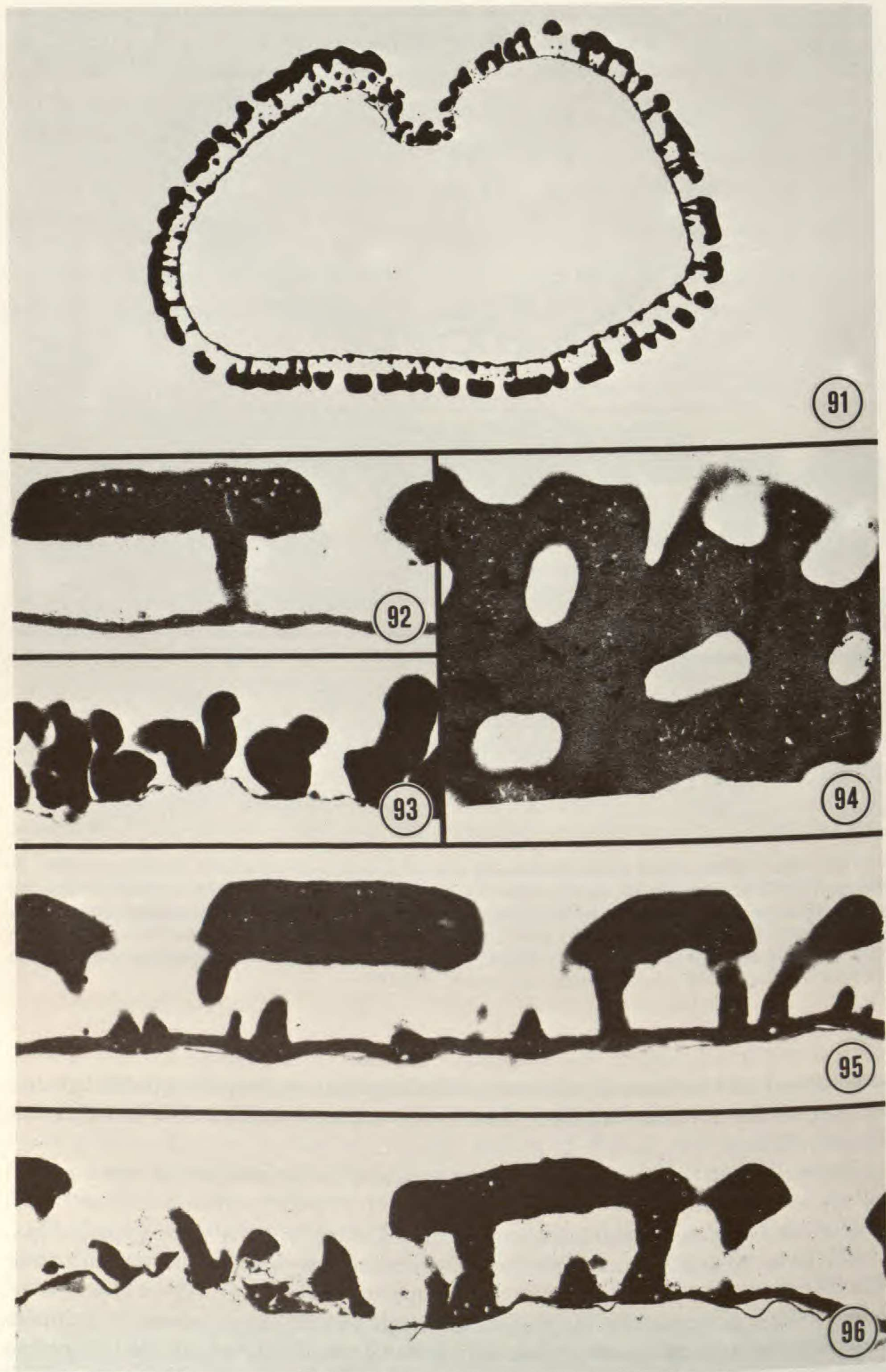
Exine Sculpturing.—In *Compsonura* the exine is mostly reticuloid (Figs. 7, 10), less commonly definitely reticulate and then sometimes with finely banded muri (Fig. 12). Pollen of *C. excelsa* (Fig. 11) and *C. ulei* (Fig. 12), both of which belong to section *Coniostele* with connate anthers, has decidedly larger tectal



FIGURES 87–90. TEM exine sections of *Virola weberbaueri* Markgraf (Tessmann 4339, P-2734).—87. Whole grain exine section, showing aperture at top, $\times 3,500$.—88. Nonapertural exine section, showing moderately thin, solid nexine, moderately thick columellate interstitium, and average to moderately thick tectum, $\times 20,000$.—89. Tangential section through two columellae, showing minute, spherical, intra-exinous cavities, $\times 19,000$.—90. Apertural exine section, showing extremely thin nexine and reduced and much disorganized sexine, $\times 10,000$.

perforations and is more semitectate-reticulate than is the pollen of the species of *Compsonura* which belong to section *Compsonura* (Figs. 7–10), which has distinct anthers.

The pollen of *Virola* exhibits a great range of exine sculpturing types and in fact its species may be divided into three different pollen types based upon differences in exine sculpturing patterns (Table 1). Species of Pollen Type I (Figs. 43–49) have basically tectate-perforate pollen grains, although sometimes they may be more or less reticuloid in their sculpturing (Figs. 47, 49). The exine of pollen in this group is usually psilate, although sometimes conspicuous granules may be present on the surface (Fig. 48). Pollen Type II is characterized by pollen which is tectate-perforate to semitectate and which has banded (Figs. 50–52) to



beaded (Figs. 53–54) muri, that occasionally may even have bands which are coarsely granulate (Figs. 55–57). Pollen of the last type, Pollen Type III, is semi-tectate-reticulate and has psilate muri (Figs. 58–64). Occasionally *Virola* pollen, especially in species with Type III pollen grains, has evident, free-standing columellae that are visible through the lumina of the reticulum, e.g., *V. multiflora* (Fig. 63) and *V. venosa* (Figs. 42, 64).

Exine Structure.—*Compsonaura* (Figs. 13, 20, 23) and *Virola* (Figs. 65, 74, 79–80, 85, 88, 92, 95) have a columellate exine, although frequently the columellae in both genera are only weakly attached to the basal nexine and may even leave circular depressions in its surface upon separation (Figs. 14, 71). Often the columellae in these two genera appear to be pendulous (Figs. 15, 69, 74, 80) from the inner surface of the tectum, which frequently exhibits granules (Figs. 16, 66–67) as well as columellae.

In the nonapertural exine *Compsonaura* generally has an average nexine, an average to moderately thick interstitium, and an average tectum (Figs. 15, 20, 23), while in *Virola* on the average the nexine is generally very thin, the interstitium is moderately thick, and the tectum is average to moderately thick (Figs. 66–67, 74, 79–80, 85, 88, 92, 95). In *Virola* the nexine may be either partially finely lamellate (Figs. 74, 79–80) or essentially solid (Figs. 85, 88), while in *Compsonaura* the nexine is generally essentially solid (Figs. 20, 23).

Small, spherical, intra-exinous cavities are frequently very conspicuous in the pollen of *Virola* (Figs. 74, 76–77, 79–80, 82–83), although sometimes they may be less conspicuous (Figs. 92, 94–96) or almost absent (Figs. 85, 88–89). Although in *Compsonaura* such intra-exinous cavities are also basically present, they are always inconspicuous (Figs. 20, 23).

In both genera the apertural exine has an extremely to very thin nexine and a reduced and much disorganized sexine (Figs. 19, 21–22, 24, 73, 75, 78, 81, 84, 86–87, 90–91, 93, 96).

Exine Stratification.—The exine in both *Compsonaura* and *Virola* is wholly ektexinous and no endexine is present.

CONCLUSIONS

Study of the pollen of the American myristicaceous genera *Compsonaura* and *Virola* supports the idea that these two genera are closely related. Palynological features which they have in common include (1) sulcate apertures, (2) usually boat-shaped and frequently more or less triangular, heteropolar, bilateral pollen grains, (3) medium-sized to small pollen, (4) reticuloid to reticulate exine sculp-

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FIGURES 91–96. TEM exine sections of *Virola* Aubl.—91–94. *V. sessilis* (A. DC.) Warburg (*Malme 2007b*, P-2730).—95–96. *V. koschnyi* Warburg (*Peck 373*, P-1985).—91. Whole grain exine section, showing aperture at top, $\times 3,300$.—92, 95. Nonapertural exine sections, showing very thin, essentially solid nexine, moderately thick columellate interstitium, and average to moderately thick tectum; note minute, spherical, intra-exinous cavities; 92, $\times 19,000$, 95, $\times 13,000$.—93, 96. Apertural exine sections, showing extremely thin nexine and reduced and much disorganized sexine, note fine nexinous lamellae to the right in Fig. 96; 93, $\times 16,000$, 96, $\times 15,000$.—94. Nonapertural exine tangential section through tectum, showing minute, spherical, intra-exinous cavities, $\times 15,000$.

turing that sometimes consists of banded or even beaded muri, (5) columellate exine structure with columellae that are weakly attached to the nexine, (6) tectate-perforate to semitectate pollen grains, and (7) apertural exine with an extremely to very thin nexine and a reduced and disorganized sexine that results in an aperture which is sharply delimited externally.

Within *Compsoeura*, pollen of the florally more advanced section *Coniostele* (Figs. 5–6, 11–12) is decidedly more advanced than that of the florally more primitive *Compsoeura* section *Compsoeura* (Figs. 1–4, 7–10).

Virola has a wide range of exine sculpturing patterns (Figs. 43–64), which allow recognition of three groups of species within the genus based on pollen morphology. To a certain extent these pollen groups show some degree of correlation with the species groups proposed by Smith (1938) (cf. Table 1). For example, all species of *Virola* with Type I pollen fall in Smith's Species Groups 1, 2, or 3 except for *V. duckei*, which has Type I pollen but is a member of Smith's Species Group 4. Only two examined species in Smith's Species Groups 1, 2, and 3 did not possess pollen of Type I, and these two species (*V. calophylloidea* and *V. weberbaueri*) both have pollen of Type II. Interestingly Smith (1938) stated that the shape of the staminate perianth of *V. weberbaueri* was not typical of his Species Group 2 and he therefore also keyed this species in his Species Group 5, which not only has pollen exclusively of Type II or III but which also contains *V. pavonis*, which has pollen with the same kind of distinctive granulate-banded muri as occur in *V. weberbaueri* (cf. Figs. 55–57). Except for *V. duckei* as mentioned above, all examined members of Smith's Species Groups 4, 5, and 6 have pollen of Type II or III.

Within the *Virola* species which have Type II pollen grains, pollen of *V. glaziovii* (Fig. 50), *V. malmei* (Fig. 51), and *V. carinata* (Fig. 52) is only very faintly banded, while pollen of *V. surinamensis*, *V. minutiflora*, *V. flexuosa*, and *V. multinervia* (Fig. 53) is more pronouncedly banded. The banded muri of the pollen of *V. calophylloidea* (Fig. 54) is more or less distinctive, while the coarsely granulate-banded muri of the pollen of *V. weberbaueri* (Figs. 55, 57) and *V. pavonis* (Fig. 56) sets these two species apart. Within the species with Type III pollen, *V. sessilis* (Fig. 58) and *V. subsessilis* (Fig. 59) have a slightly different type of exine sculpturing pattern that seems to set these two species somewhat apart from the other species with Type III pollen grains.

Interestingly, the small, spherical, intra-exinous cavities that are generally present in the sexine of *Virola* pollen grains are very conspicuous in the pollen of *V. divergens* (Figs. 74, 76–77) and *V. peruviana* (Figs. 79–80, 82–83), both of which belong to Pollen Type I, while these cavities are less conspicuous in the pollen of *V. sessilis* (Figs. 92, 94) and *V. koschnyi* (Figs. 95–96), which belong to Pollen Type III, and they are inconspicuous in the pollen of *V. carinata* (Fig. 85) and *V. weberbaueri* (Figs. 88–89), which belong to Pollen Type II. Also the nonapertural nexine in *V. divergens* (Fig. 74) and *V. peruviana* (Figs. 79–80) with Type I pollen is more conspicuously lamellate and thinner than the nonapertural nexine in *V. carinata* (Fig. 85) and *V. weberbaueri* (Fig. 88), which both have Type II pollen grains, while the nonapertural nexine of both *V. sessilis* (Fig. 92) and *V. koschnyi* (Fig. 95), which belong to Pollen Type III, is as thin as the nexine in *V. divergens* and *V. peruviana* but not as pronouncedly lamellate.

Although the pollen of the palynologically most primitive species of *Compsonera* and *Virola* is externally more or less indistinguishable (cf. Figs. 1–2 and 7 of *Compsonera capitellata* with Figs. 25 and 43 of *Virola calophylla*), pollen of *Compsonera* can be separated from that of *Virola* on the basis of the following characters: (1) the thickness of the nonapertural nexine in *Compsonera* pollen is average, with the nexine constituting about a third of the total exine thickness (Figs. 20, 23), while the nonapertural nexine in *Virola* (Figs. 74, 79–80, 85, 88, 92, 95) is generally very thin and usually makes up less than 15% of the total thickness of the nonapertural exine, (2) the nexine may be more or less conspicuously lamellate (Figs. 74, 79–80, 96) or not (Figs. 85, 88, 92) in *Virola* (although nexinous lamellae are significantly most conspicuous in the species of *Virola* which are sculpturally most similar to *Compsonera* such as *V. divergens* and *V. peruviana*), while nexinous lamellae are always more or less inconspicuous in *Compsonera* (Figs. 20, 23), and (3) spherical, intra-exinous, sexinous cavities are generally conspicuous in *Virola* (Figs. 74, 76–77, 79–80, 82–83, 92, 94, 95–96), especially in the species which are sculpturally most similar to *Compsonera*, while such cavities are very inconspicuous in *Compsonera* (Figs. 20, 23). The markedly semitectate-reticulate pollen of the palynologically more advanced species of *Virola* (Figs. 50–64) which belong to Pollen Types II and III of course are usually readily distinguishable from the pollen of *Compsonera* section *Compsonera* (Figs. 7–10), although pollen of *Compsonera* section *Coniostele* (Figs. 11–12) might be confused (at least externally) with the pollen of some species of *Virola* which possess Type II pollen grains (cf. Fig. 12 of *Compsonera ulei* pollen with Figs. 51 and 53 of *Virola malmei* and *V. multinervia* pollen).

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